

CHAPTER 4-1

ADAPTIVE STRATEGIES: PHENOLOGY, WHAT DOES IT MEAN?

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CHAPTER 4-1

ADAPTIVE STRATEGIES: PHENOLOGY, WHAT DOES IT MEAN?



Figure 1. *Hylocomium splendens* emergent from the winter snow. Timing of reproduction must be such that sperm do not mature on a warm day in winter, only to be frozen by ensuing sub-freezing temperatures. Photo by Michael Lüth, with permission.

Phenology, defined by Stark (2002) as "the study of the timing of growth and reproductive events," is also used to refer to the series of events and includes changes of form and phenomena of an organism through time as they relate to climate and season. Classical studies in Europe have included branching architecture, timing of vegetative growth, gametangial initiation times, fertilization times, duration of sporophyte development, and time of spore liberation (Stark 2002). To these we can add nutritional status, population dynamics, fitness measures, spore dispersal patterns, interplay of sexual and asexual reproduction, **sexual dimorphism** (sexes look different), structural development, dormancy, and desiccation tolerance. Studying phenology permits us to understand interplay of plants with a constantly changing environment.

In the temperate forest, trees lose leaves in autumn, bloom and leaf out in spring, and store **photosynthate** (product of photosynthesis) in summer. These canopy phenological events have profound impact on smaller

plants growing beneath them. Spring flowers bloom before leaves emerge on trees, taking advantage of a nearly full complement of sunlight. A few shade-tolerant species grow more slowly and take advantage of the tree canopy to protect them from bright light of summer. Other species use fungal partners to connect them with trees, taking advantage of canopy photosynthate that permits them to survive in low light. As these ground cover taxa enlarge through summer, bryophytes are impacted by light-depriving leaves of larger neighbors.

Bryophytes also must cope not only with a changing light and moisture regime resulting from the direct effect of changing seasons, but also with microclimatic changes resulting from changes in the tracheophytes around them. Their C_3 photosynthetic pathway (CO_2 is immediately put into photosynthesis, forming 3-C compound) permits them to take advantage of early light and moisture at snowmelt (Figure 1) when low temperatures prevent even other C_3 plants from having effective photosynthesis.

Bryophytes are limited in their occupancy of deciduous forests by the phenological event of leaf fall that fully blocks the light essential for their photosynthesis. Most forest bryophytes are perennials, yet, unlike their tracheophyte counterparts, most are unable to avoid the changing seasons by storing energy underground and losing their photosynthetic parts. As C_3 plants, they are able to photosynthesize at low temperatures as soon as the snow is gone, but they are likely to find the hot temperatures of summer to be detrimental. Furthermore, they require water to transfer their swimming sperm, rarely having an animal vector to carry these for them. Based on these constraints, we should expect that bryophytic phenological responses differ somewhat from those of their lignified vascular companions as the bryophytes take advantage of or avoid the changes provided by these companions.

One need only examine a few bryophyte floras to recognize that phenological events for mosses are poorly documented. Almost any flowering plant flora will include flowering dates, but bryophyte floras from Japan (Noguchi 1987-1994), the Nordic (Nyholm 1986, 1898, 1993), Michigan (Crum 2004), and the tropics (Gradstein *et al.* 2001) all fail to mention any season for any life cycle event, even the season of spore dispersal. Crum and Anderson (1981) occasionally include the season of spore ripening for the Eastern United States, but never any information on seasons for other events. In treating the genus *Sphagnum*, for which both authors are world-renowned systematists, not a single species of the 42 described includes any phenological information. Conard (1947), in reporting the phenology of Iowa bryophytes, was able to find dates in the literature for presence of antheridia or archegonia for only 15 taxa out of 292. He was more successful in finding documentation of capsule production dates, locating it for all but 28 of the taxa that fruit in Iowa.

As the young field of bryophyte ecology began taking shape in the early 1970's, Longton (1974) suggested that the International Association of Bryologists and the British Bryological Society (Longton 1982) embark upon bryophyte phenology as a project. Perhaps because of British national pride, or because of the large number of good bryologists among the British society's mostly amateur membership, such a project had appeal to the BBS. It was a way for many people to contribute important information that could only be gained by such a wide undertaking. Through consorted efforts, they could define not only the phenology of a wide array of species, but could look at differences in patterns throughout the British Isles, comparing inland species with coastal, mountain and moor with valley and field.

Developing Consistency in Reporting

For comparisons among various studies and localities, a consistent way of examining and describing life cycle stages is necessary. Again, the British were the leaders, with a publication by Greene (1960) elucidating the stages. The British faithfully followed this nomenclature in making their reports. Slight modifications and refinements have made this system workable around the world.

Most researchers seem to recommend observing every two weeks to elucidate the phenology (Stark 1984). In general, the life cycle stages are arrested while the plants are dry, so it is possible to collect specimens periodically,

then examine them later at one's convenience. The ability of bryophytes to continue their life cycle upon rehydration makes it possible to identify the stages after rehydration and even to photograph them. Nevertheless, one should exercise caution if high resolution is needed in defining dates because the ability to retain water may permit the bryophytes to continue development for a period of time. Mosses kept in plastic bags may continue growth for a month, elongating abnormally in the lower light of their new location. Dry mosses may shed the operculum prematurely, since drying itself is needed in most taxa to constrict the capsule and force the operculum off, occurring sooner in the dry lab than it would in nature with nightly dew to re-supply moisture.

When reviewing a series of dry collections, Stark (1984) recommends soaking the stems for a few minutes and removing the leaves on the upper 10-15 mm of the main stem, but not from the branches. This can be done with microforceps by holding the tip and pulling the leaves downward toward the base, being careful not to injure the gametangia in the process. Once leaves are removed, one can carefully remove a group of gametangia near the apex and place it in a drop of water on a slide. In **pleurocarpous** mosses (Figure 1), gametangia occur on side shoots, rather than at the stem apex where they occur in **acrocarpous** mosses (Figure 5). You can shorten the process by pressing the gametangia off with the side of a probe. In either case, use a cover slip and examine them with the compound microscope. Data should be recorded using one of the published systems of naming stages.

System of Naming

Fortunately for the British, and for bryologists everywhere, systems for scoring the developmental stages already existed. Greene made the "most significant" contribution to phenology (Stark 2002) when he suggested 20 stages (Figure 2), centering on the reproductive phases only, and omitting any presentation of the spore and protonema. He even recommended a method for preparing figures to illustrate the monthly changes (Figure 3).

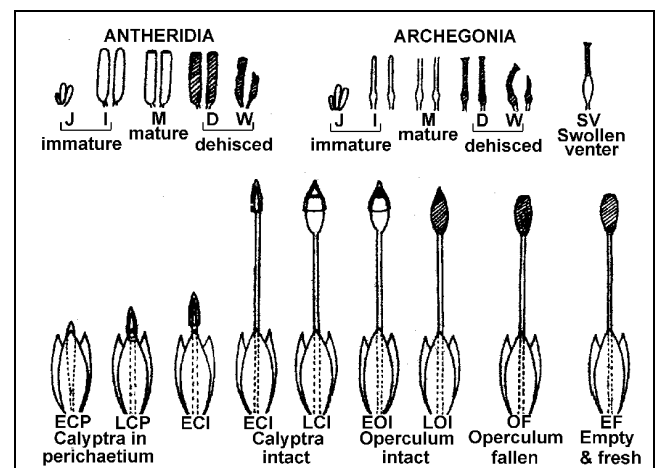


Figure 2. Maturation stages as represented by Greene (1960). J = juvenile, I = immature, M = mature, D = dehiscent, W = withered archegonia or antheridia, SV = swollen venter, ECP = early calyptra in perichaetium, LCP = late calyptra in perichaetium, ECI = early calyptra intact, LCI = late calyptra intact, EOI = early operculum intact, LOI = late operculum intact, OF = operculum fallen, EF = empty and fresh.

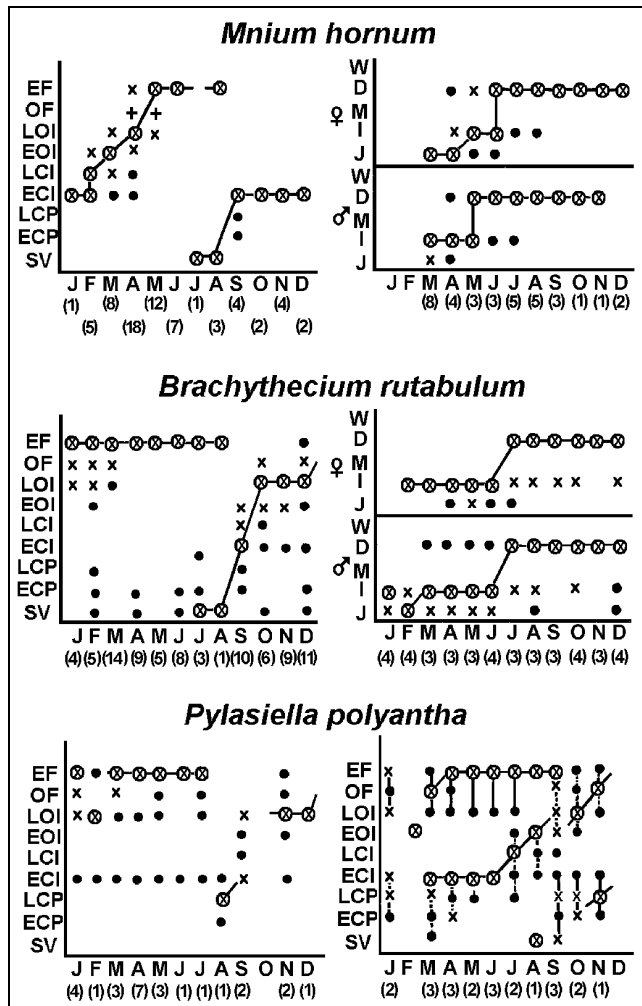


Figure 3. Sample figure given by Greene (1960) to illustrate the gametangial and capsular cycles of three species of moss. **Numbers in parentheses** indicate number of collections in which the majority state occurred. The **circled x** represents the state that was clearly the most abundant, **x** alone represents other stages that occurred as majority states in some collections, and a **solid circle** indicates present but never abundant. As in the previous figure, **SV** = swollen venter, **ECP** = early calyptra in perichaetium, **LCP** = late calyptra in perichaetium, **ECI** = early calyptra intact, **LCI** = late calyptra intact, **EOI** = early operculum intact, **LOI** = late operculum intact, **OF** = operculum fallen, **EF** = empty and fresh; **J** = juvenile, **I** = immature, **M** = mature, **D** = dehiscent, and **W** = withered archegonia or antheridia.

Shortly thereafter, Forman (1965) developed a somewhat easier system by which researchers could make consistent descriptions related to phenological events. He decided that no two stages should be named separately unless they were morphologically distinct. Furthermore, the stages should be relatively easy to recognize without the use of a microscope. He defined the life cycle in 12 stages (Figure 4) for the purpose of describing the phenology and other events more precisely and in a standard fashion.

Forman (1965) decided that stages need not be delimited if they did not require any change in environmental conditions. For example, early and late stages of seta elongation are not separated because they occur as a continuous process independent of any environmental trigger. On the other hand, growth of the

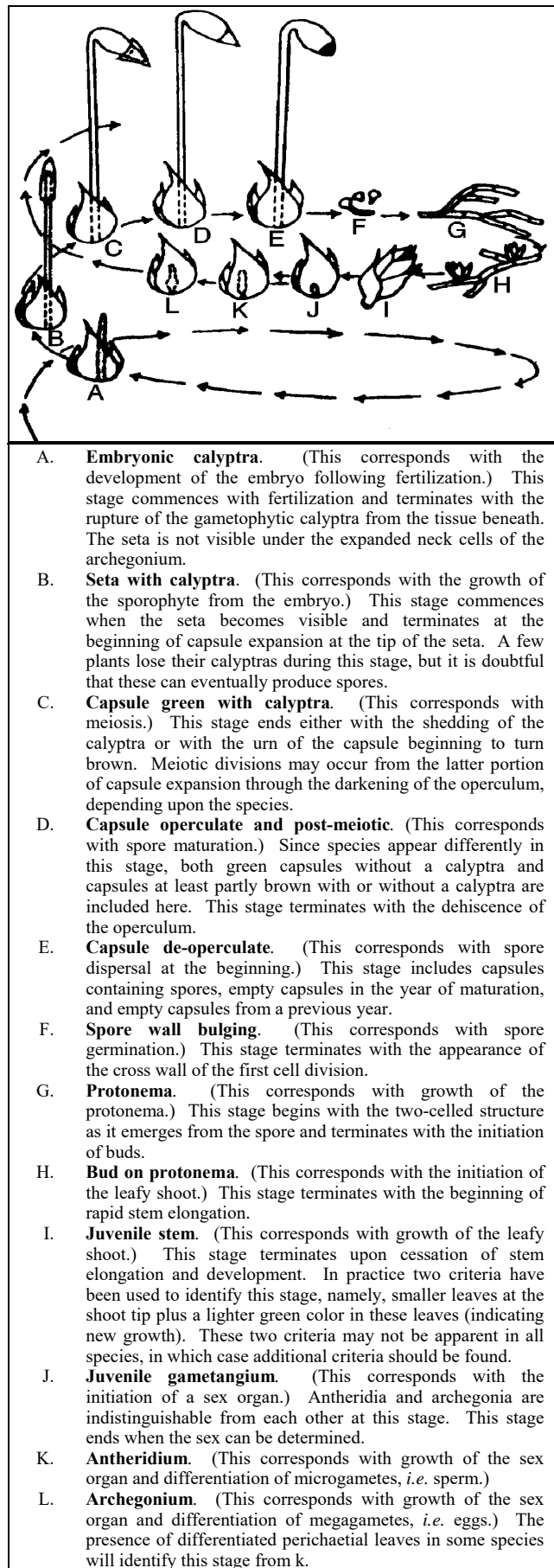


Figure 4. Life cycle stages based on Forman (1965).

embryo within the perichaetium is likely to differ from growth of the seta because the developmental environment changes substantially once the seta emerges from the protective leaves. Forman conveniently chose the embryonic calyptra as the first stage (of course there is no beginning or end to a cycle), placing the protonema to gametophore stages (including production of gametangia) last, perhaps because these "later" stages are the most difficult and least likely stages to be observed.



Figure 5. *Bryum pallescens* showing terminal seta and capsule of an acrocarpous moss. Note that the capsule is protruding from last year's gametophyte while the growth for the current year is tall. Photos by Michael Lüth, with permission.

Stark (1984), in encouraging North Americans to join in collecting phenological data, recommended a modification of the systems of Longton (1979) and Greene (1960) for describing gametangia. It adds clarity and distinguishes between young, mature, and ruptured gametangia, distinctions that are important in taxa that have gametangial development interrupted by winter or a dry season:

- 1 = unruptured and less than 1/2 full length
- 2 = unruptured and more than 1/2 their full length
- 3 = green or hyaline with apices ruptured
- 4 = brown with apices ruptured

A = abortive; brown and unruptured

Stark later (2002) developed a system of fourteen events, but this system requires a 400x lens to distinguish the beginnings of gametangia before the gender is distinguishable, and while it provides more information, such requirements as determining that the theca contains fewer than half the spores makes the system rather impractical.

Imura (1994) reduced the number of stages to five in his study of *Pogonatum inflexum*, but provided us with a graphical way of representing the sequence of events that is easy to produce and useful in understanding phenological relationships across multiple years (Figure 6). The degree of detail needed depends on the purpose, and certainly the representation by Imura serves a useful purpose to see the progression and overlap of events between years.

While the stages of the life cycle are similar for all bryophytes, the timing differs. This chapter will examine the major events and factors that control their timing. As demonstrated by Imura (Figure 6), these events include gametophyte growth, production of gametangia, fertilization, production of sporophytes, and dispersal of spores, as well as events that are more difficult to examine in the field – spore germination and development of gametophore buds.

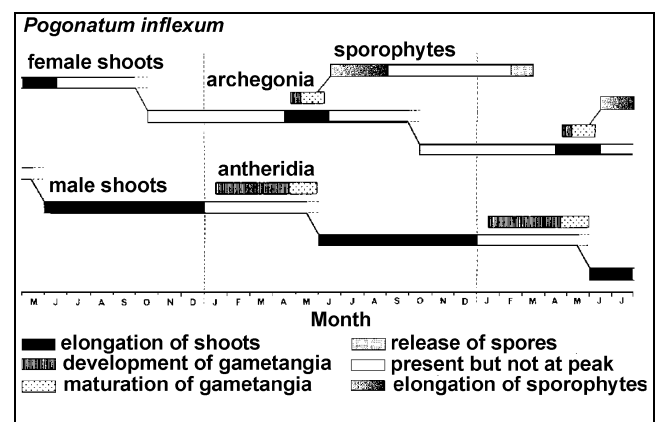


Figure 6. Annual sequence of events for *Pogonatum inflexum* on Miyajima Island, Japan. Redrawn from Imura (1994).

Summary

Phenology is defined by Stark (2002) as "the study of the timing of growth and reproductive events." The term is likewise used to refer to the series of events and includes changes of form and phenomena of an organism through time as they relate to climate and season.

The life cycle of a bryophyte can be described based on those stages that are **observably different**, are **discontinuous**, and require a **change in environmental conditions**. This definition presents us with the recognizable stages of **embryonic calyptra**, **seta with calyptra**, **green capsule with calyptra**, **operculate post-meiotic capsule**, **de-operculate capsule**, **spore with bulging wall**, **protonema**, **protonema with bud**, **juvenile stem**, **antheridium**, **archegonium**.

Acknowledgments

I appreciate the helpful comments of Heather Smith in giving me a student's perspective on this chapter. Linda Luster checked the literature citations, proofread, and checked for needed glossary entries.

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CHAPTER 4-2

ADAPTIVE STRATEGIES: PHENOLOGY, IT'S ALL IN THE TIMING

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Figure 1. *Atrichum undulatum*, emergent from the snow, has already formed capsules, but must time the release of spores for a time favorable for their dispersal and germination. Photo by Michael Lüth, with permission.

Timing the Stages – Environmental Cues

It's all in the timing! Life cycles are the acrobatics of the plant world, and failure to time things correctly is just as deadly as missing your partner when swinging on the high wires. Timing determines when to germinate, when to release sperm, when to develop the sporophyte, and when to release the spores. This timing must be closely attuned to the climate of the area where the organism is growing and is a major factor in limiting the distributions of many species. In 1984, Taylor and Hollensen contended that there is "rarely any attempt to correlate life changes with time of year." However, where this ecophysiological information is lacking, there is no shortage of studies on dates of phenological events, despite their absence in most bryological manuals. In fact, the sheer numbers of studies are daunting and have caused the delay of this chapter. I will attempt to provide some of the implications of cause

and effect through that available literature and examine how habitat and geography influence the timing.

Patterns

Stark (2002a) has compiled patterns of temperate zone phenology based on publications of a few bryophytes [*Pohlia* in UK, *Ptychomitrium* in Japan, *Grimmia laevigata* in Spain, *Bryum argenteum* in UK, *Polytrichum strictum* (as *P. alpestre*) in UK, *Forsstroemia producta* in eastern USA]:

1. Antheridia initiate in autumn and winter, maturing the next spring and summer (duration several months)
2. Archegonia initiate and mature in the same spring and summer (duration several weeks)
3. Fertilization occurs in summer, lasting two weeks to several months.

This pattern most likely works well for the many bryophytes that live in areas where they rely on spring rains for fertilization. But notable exceptions exist to these examples with their strongly temperate bias. For example, in Brazil the period of fertilization for *Sematophyllum subpinnatum* (Figure 2) extends throughout the entire year (de Oliveira & Pôrto 2001). In the desert, both gametangial initiation and fertilization in *Trichostomum sweetii* occur in the autumn and winter (Stark & Castetter 1995).



Figure 2. Epiphytic moss *Sematophyllum subpinnatum* in Brazil. Photo by Michael Lüth, with permission.

The sporophyte is dependent on moisture for its own development, but it fares best if it is dry for spore dispersal. Stark (2002a) considered that six generalized patterns prevail for sporophyte maturation:

1. Fertilization in spring and summer with continuous development; spore dispersal anywhere from early summer to the following spring; suitable for a mild climate.
2. Fertilization in summer; embryos overwinter & sporophyte matures the following spring or summer; spore dispersal over extended period; typical of areas with harsh winter; two cohorts may be developing at the same time.
3. Fertilization in summer (or spring) with continuous development to or just past meiosis; overwintering in meiotic/postmeiotic phase; spore dispersal winter-spring; known in south temperate of Northern Hemisphere.
4. Fertilization in winter/spring with embryos forming first winter; dormancy in summer; sporophyte maturation second winter; known in several desert species.
5. Annual species, sporophyte development within two months; fertilization at various times of year – flexible.
6. No pattern; events throughout the year

Zander (1979) reported patterns with taxonomic affinities. He examined spore maturation times in the **Pottiaceae** and showed that differences tended to group by suprageneric taxa. The **Trichostomoideae** mature primarily in spring, **Pleuroweisieae** in midyear, **Barbuleae** are bimodal, **Pottiaceae** primarily spring, but also summer and winter, **Cinclidotoideae** spring and summer, and **Leptodontieae** poorly known but mainly spring. He attributed the patterns to regional climate and the stress-tolerant nature of these taxa. He further considered that their **ruderal** (waste areas) habitat subjected them to competition from annual tracheophytes that forced them to take advantage of snowmelt water. He further concluded

that spores of nearly all mid-latitude Pottiaceae taxa of variable, dry, lowland habitats mature in winter, spring, or early summer. Yet these taxa typically take 9 to 12 months for their sporophytes to mature. Perhaps this strategy permits the spores to germinate immediately while there is still available water, space, and light. Those species that occur in seepage areas or near waterfalls have summer or autumn maturation times instead, again suggesting that water is a driving force in sporophyte maturation times for the other taxa. Zander also found that non-endemic dioicous taxa in the Pottiaceae retain mature capsules slightly longer (mean 6.77 months) than do monoicous taxa (mean 5.55 months).

Growth

Growth is generally controlled by a combination of factors (light, temperature, nutrients, water), but in bryophytes, available water generally is the most important (Zehr 1979). Once moisture is available, the temperature must be sufficiently warm for the water to be in liquid form. Since bryophytes are C_3 plants, most function best at temperatures less than 25°C, so growth may cease during summer.

In temperate climates, growth generally seems to occur in spring and autumn, ceasing or at least diminishing in summer (Al-Mufti *et al.* 1977). For example, *Atrichum undulatum* (Figure 1) exhibits this type of growth in South Wales (Figure 15; Benson-Evans & Brough 1966). For other species, growth is predominately in spring, and autumn seems to be a time for elongation without biomass production (Rincon & Grime 1989; Figure 3). Other taxa, adapted to full sun, may be more productive in summer. This is the case in *Polytrichum juniperinum* (as *P. alpestre*; Figure 4), which grows in June and July (Longton 1979). Interestingly, dry weight continues to increase until September, despite the greater increase in photorespiration with rising temperature, a topic that will be discussed in more detail in the chapters on photosynthesis and productivity.

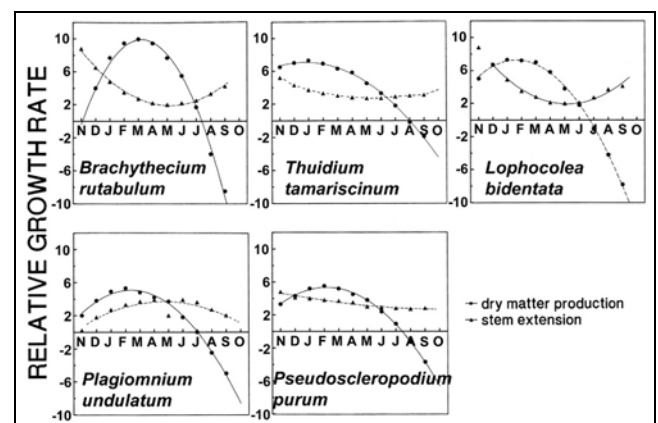


Figure 3. Comparison of relative growth rates in length and dry matter production in five bryophytes from calcareous grasslands. Redrawn from Rincon & Grime (1989).

Where winters are mild, growth may occur throughout the winter. In Japan Imura and Iwatsuki (1989) found that male plants of *Trachycystis microphylla* (Figure 5) elongate most rapidly from October until January, but interestingly, the female plants begin their rapid elongation in January and continue until June. In cases where this

makes male plants taller than females during sperm dispersal stages, this could be an advantage for facilitating splash of sperm onto an archegonial inflorescence.



Figure 4. *Polytrichum juniperinum*. Photo by Janice Glime.



Figure 5. *Trachycystis microphylla*, a species in which male and female plants elongate at different times. Photo by Li Zhang, with permission.

Epiphytes may take advantage of decreased desiccation and temperature in winter. Pitkin (1975) found the greatest growth of *Hypnum cupressiforme* (Figure 6), *Platygyrium repens*, *Neckera pumila* (Figure 7), *Isoetecium myosuroides* (Figure 8), and *Homalothecium sericeum* in November to January in Oxfordshire, UK, corresponding to highest rainfall and mean temperatures below 10°C at 15:00 hours. Trynoski and Glime (1982) suggested that the appearance of more bryophytes on the south side of trees at breast height in the Keweenaw Peninsula of Michigan, USA, could indicate they were able to grow in winter when protection and moisture were available in the space between snow and tree trunk.

Furness and Grime (1982) show strong seasonal effects of temperature that help to explain the phenology of some bryophytes (Figure 9). These results are consistent with peaks of growth in spring and autumn in British tall herb communities. But they also show that different parts of the bryophyte can grow at different times and be favored by different temperatures. In *Brachythecium rutabulum* (Figure 10) growth of rhizoids peaks at 12°C, branches at 15°C, and stems at 20°C.



Figure 6. *Hypnum cupressiforme* in its epiphytic habitat. Photo by Dick Haaksma, with permission.



Figure 7. Epiphytic habitat of *Neckera pumila*. Photo by Jan-Peter Frahm, with permission.



Figure 8. *Isoetecium myosuroides* on tree at Swallow Falls, Wales. Photo by Janice Glime.

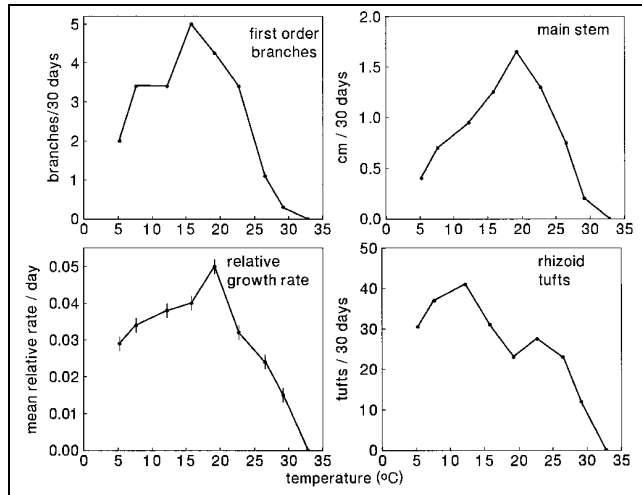


Figure 9. Effects of lab temperature on growth of branches, stems, and rhizoids of *Brachythecium rutabulum* (Figure 10) and relative growth rate among 9 growth temperatures under conditions of constant humidity. Redrawn from Furness & Grime 1982.



Figure 10. *Brachythecium rutabulum*. Photo by Michael Lüth, with permission.

This difference in temperature, and thus timing of life processes, is consistent with observations on *Fontinalis* organs (Glime 1980, 1982, 1987b) and suggests that the bryophyte apportions its limited photosynthate to different activities at different times. This conserves energy and permits directing that energy into the needed structures. In *Fontinalis*, we can presume that the timing is advantageous because the rhizoids develop best at temperatures that coincide with the season when the moss is most likely to be stranded above water during low water (summer) and is therefore not likely to be dislodged by the motion of the water. The plants are typically "glued" to the rocks by their covering of sticky algae at this time. Furthermore, in *Fontinalis* branching and growth follow the season of maximum runoff when fragments have been delivered to new substrata in the stream. Intact but damaged plants can also be replenished then (Glime *et al.* 1979; Glime 1980; Figure 11). Timing of gametangial production must permit the gametes to be splashed from plant to plant without having these structures submersed where they will be carried away by the moving water in streams.

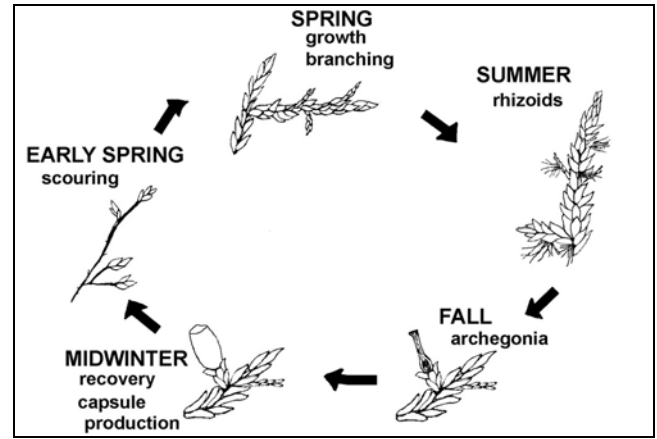


Figure 11. Phenological cycle of growth and reproduction in *Fontinalis dalecarlica* and *F. novae-angliae*. Drawings by Janice Glime.

Many bryophytes, such as *Eurhynchium praelongum* (Figure 12), are relatively dormant in winter, resuming growth in spring (April) and continuing through August, with the main peaks in May and September (Benson-Evans & Brough 1966). The common boreal forest feather moss *Pleurozium schreberi* (Figure 13) grows little in winter, with growth from April to November (Longton & Greene 1969), but then one can't expect it to grow in the dim or absent light under snow.



Figure 12. *Eurhynchium praelongum* Bicton Common England. Photo by Janice Glime.



Figure 13. *Pleurozium schreberi*, a moss that spends its winter under snow and resumes growth when the snow melts. Photo by Janice Glime.

In contrast, Mishler and Oliver (1991) found that **innovations** (new shoots; in acrocarpous mosses, a new branch) in the drought-tolerant *Syntrichia ruralis* (in the mountains of southern New Mexico, USA) (Figure 14) appeared in midwinter, lengthening slowly throughout spring, but growing rapidly in late summer and completing growth by winter. Likewise, the chlorophyll concentration was higher in late summer and winter than it was in early summer, but there was no regular pattern of chlorophyll *a/b* ratios.



Figure 14. *Syntrichia ruralis* benefitting from the rain. Photo courtesy of Peggy Edwards.

Other species in these temperate climates lack seasonal growth peaks. Benson-Evans and Brough (1966) found that *Funaria hygrometrica* (Figure 27) initiated new leafy shoots continuously throughout the year in South Wales, reaching their maximum height of about 5 mm in 10 weeks (Figure 15). This results in numerous shoots that can quickly colonize bare ground.

Sphagnum most likely is controlled primarily by water availability, not by temperature. Lindholm (1990) demonstrated that the hummock species *S. fuscum* could grow at most normal temperatures above 0°C, but that moisture was the primary determinant in that range. Li (1991) found that 30-35°C was optimum for growth of the hummock-dwelling *Sphagnum papillosum* and *S. magellanicum* when adequate water was available.

In South Wales, *Atrichum undulatum* (Figure 1) becomes dormant in late summer and begins growth again

in January (Figure 15). Benson-Evans & Brough 1966). Different clones of this species can have different growth periods. In *Funaria hygrometrica* (Figure 27), growth can begin from new plants in any month of the year and is relatively continuous (Figure 15).

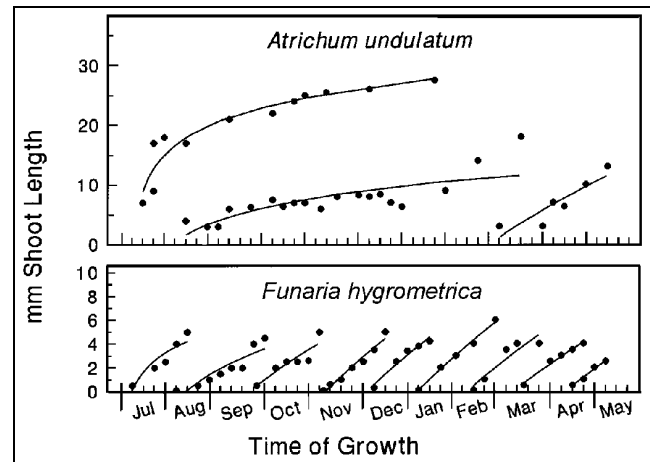


Figure 15. Contrast in vegetative growth periods for two bryophyte species in South Wales. *Atrichum undulatum* (Figure 1) becomes dormant in late summer and begins growth again in January. The three curves follow three different sets of plants. In *Funaria hygrometrica*, growth can begin from new plants in any month of the year and is relatively continuous. Redrawn from Benson-Evans and Brough (1966).

The leafy liverwort *Lophozia ventricosa* var. *silvicola* (Figure 16) seemed to exhibit no change in shoot density during the growing season (Laaka-Lindberg 1999). Measurements on liverworts are rare, and for the many very small species, very difficult.



Figure 16. *Lophozia ventricosa* with gemmae, a species that does not seem to change shoot density during the growing season. Photo by Jan-Peter Frahm, with permission.

One factor that may play a role in seasonal changes in growth is chlorophyll concentration. Valanne (1984) felt chlorophyll concentrations did not change seasonally. On the other hand, Raeymaekers and Glime (1986) found that chlorophyll concentrations in *Pleurozium schreberi* (Figure 13) were slightly higher in summer than in early spring or late autumn. This is not surprising as the plants are shielded from light by snow in winter, thus being unable to replace chlorophyll. The heat and drought of summer can likewise reduce the ability to replace damaged

chlorophyll. Habitats can affect the seasonal changes in chlorophyll content of bryophytes. For example, the forest species *Brachythecium rutabulum* (Figure 10) has seasonal chlorophyll changes (Kershaw & Webber 1986), increasing as the summer progresses and the light penetration decreases. Epiphytic bryophytes likewise respond to the decreasing light penetration through the canopy (Miyata & Hosokawa 1961). For the aquatic moss *Fontinalis* (Figure 17), both light intensity and temperature may play a role in the observed seasonality of chlorophyll content (Bastardo 1980).



Figure 17. *Fontinalis antipyretica*, a moss that grows in cooler weather. Photo by Andrew Spink, with permission.

Growth in most bryophytes is limited by water availability, with light, nutrients, and temperature playing lesser roles. Most grow best at temperatures below 25°C and go dormant above that. This puts most of their growth in temperate zones in spring and autumn, while permitting winter growth in warmer climates and summer growth in Polar Regions. Growth in mass can precede growth in length, and this may even be a general rule. Chlorophyll concentrations respond to changes in light intensity – a seasonal phenomenon.

Asexual Reproduction

The large number of propagule possibilities has already been discussed in the chapter on development. But what controls this production? In some species, these are so ever-present that they are used as taxonomic characters (*Plagiothecium*, *Pohlia* spp.). In fact, they may be more common than we supposed, as noted by researchers on *Orthotrichum* (BFNA 2007; Figure 18). But such propagula require energy to produce and thus we should expect some seasonal differences that avoid other large-energy-requiring events. It is well known that *Marchantia polymorpha* does not produce gemma cups while it is producing sexual reproductive structures. This is demonstrated by the suppression of gemma cup development during long-day conditions when archegoniophore development is occurring, but the addition of high sucrose concentrations can permit their development (Terui 1981). *Tetraphis pellucida* likewise does not have gemmae and female gametangia or sporophytes at the same time. Thus, we can in many cases

surmise their phenology as those seasons when sexual reproduction is not occurring.

In liverworts, it appears that many taxa lack any seasonal absence of gemmae (Schuster 1988; Duckett & Renzaglia 1993), especially in the tropics (Schuster 1988). *Lophozia silvicola* had gemmae throughout the sampling period of May to October in southern Finland, but their peak months were July through September (Figure 19; Laaka-Lindberg 1999; Laaka-Lindberg & Heino 2001).



Figure 18. Gemmae (dark spots on leaves) on *Orthotrichum obtusifolium*. Photo by Michael Lüth, with permission.

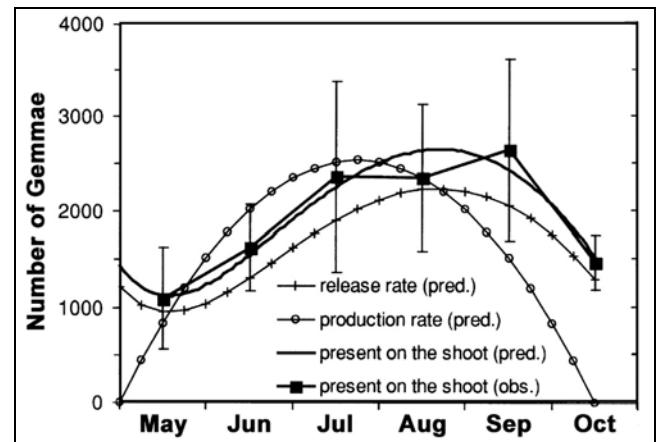


Figure 19. Model predictions (pred.) and observed behavior of gemmae from five colonies of *Lophozia silvicola* in southern Finland in 1997-1999. Redrawn from Laaka-Lindberg & Heino (2001).

Laaka-Lindberg (1999) found that gemmae of *Lophozia ventricosa* var. *silvicola* (Figure 16) was highest in early spring, declining rapidly as the end of the growing season approached. Laaka-Lindberg and Heino (2001) suggested that there is a seasonal dormancy in gemmae of *L. ventricosa* var. *silvicola*. They modelled the effects of having two types of gemmae, dormant and non-dormant. Only the dormant gemmae could be expected to survive winter. This model fit well with data for southern Finland for this species and provided a mechanism for replacement of shoots lost to winter mortality. Success would be greatest if more dormant gemmae were produced at the end of the growing season.

Response to light intensity in some taxa suggests that at least some liverwort gemma production should be seasonal. Kumra and Chopra (1989) found that maximum

gemma cup production in *Marchantia palmata* occurred at continuous light at 4500 lux. However, this is an unlikely combination in nature, with full sun at ~70,000 lux and 24-hour light occurring only in Polar Regions.

Laaka-Lindberg (2000) considered that gemmae most likely follow the same seasonal trends as vegetative growth. She reasoned that since gemmae are produced by mitotic cell divisions, albeit in specialized cells, they would be susceptible to the same environmental regulation of growth as normal gametophytic tissue. Since growth often is arrested during sexual reproduction, this is a reasonable possibility.

In west tropical Africa, two species of the moss genus *Calymperes* exhibit distinct seasonal production of gemmae (Odu & Owotomo 1982). Reese (1984) found a striking seasonality in *Syrrhopodon texanus* (Figure 20), another member of the same family, with gemmae production increasing in August and peaking in September in the Gulf coastal plain. This follows the high rainfall season in July, which could be favorable to gemma production and establishment.



Figure 20. *Syrrhopodon texanus*, a moss with seasonal gemma production that peaks in September in the Gulf coast, USA. Photo by Janice Glime.

Aside from balancing the energy needs of sexual reproduction, the asexual structures generally do not have to wait for the right season, thus providing the plant with a more reliable means of reproduction.

Gametangia

Timing of gametangial production might well be the most important timing function a **cryptogam** (any plant with an independent gametophyte) could have. With only one cell layer of protection during development, gametes begin their existence in peril. Once released, the sperm have virtually no protection and must reach the egg in a film of water before effects of sun and winds render their required watery milieu non-existent. Furthermore, it is likely that they are susceptible to UV damage, lacking even a cell wall for protection. Gamete availability itself typically lasts only 1-2 weeks (Crum 2001), and even less in some species. Hence, mechanisms that position this development at a time most likely for success are essential for this step to reach fruition.

The timing mechanisms available to bryophytes have been studied extensively in, of course, the lab rat moss, *Physcomitrella patens* (Figure 21). Hohe *et al.* (2002)

have determined that temperature, light intensity, and day length all impact the number of sporophytes produced, and thus by inference we must conclude also impact the success of the gametes. In this moss, the highest number of sporophytes resulted when the mosses were cultured at 15°C, 8:16 light:dark cycle at 20 $\mu\text{mol}/\text{m}^2/\text{s}$. Culture at 25°C or at 16-hour days drastically reduced the number of sporophytes, indicating that this species is adapted to reproducing under the conditions of spring in the temperate zone. As might be expected, growth diminished under conditions that favored reproduction. Hohe and coworkers even identified a MADS-box gene, PpMADS-S, that produced 2-3 times as much RNA under conditions that favored sporophyte development, suggesting its role in that development.



Figure 21. *Physcomitrella patens* with capsules; growth diminishes while capsules are maturing. Photo by Michael Lüth, with permission.

Laboratory experiments do not necessarily represent the real world. Day-night temperature differences may be critical, and certainly water is important. Maturation of reproduction must be timed to coincide with a season suitable for sperm transfer. For example, Odu (1981) showed that in four tropical African mosses, gametangia develop at the beginning of the rainy season. Sporophytes mature to coincide with the dry season.

Signals for timing of gametangial production are most likely a mix of direct responses to rainfall and other moisture sources and other cues, such as day length, that are generally good predictors of later environmental conditions. For example, we see in *Sphagnum* that success of sporophyte production was positively related to the precipitation the previous summer and that summer droughts had a negative influence on gametangial formation (Sundberg 2002). Even after fertilization, however, drought has a negative effect on the sporophyte by drying it too soon before the spores are mature.

In Scandinavia, this favorable season for gamete release appears to be spring (Arnell 1875), most likely taking advantage of "spring showers." Arnell (in Crum 2001) found that 15% of the taxa released gametes in January-March, 52% April-June (20% in May), 25% July-September, and 8% October-December. However, some taxa do not have a "season." Leitgeb (1868) found that *Fontinalis antipyretica* (Figure 17) formed antheridia from spring until autumn [although I found that archegonia matured in autumn and that numbers were greatest under short (6-hour) photoperiods (Glime 1984)].

In milder climates, such as California, USA, late autumn or winter months can provide the best season for successful fertilization. *Fossombronia longiseta* has mature archegonia and antheridia there in November and December (Haupt 1929b).

In Japan, Deguchi and Yananose (1989) found that *Pogonatum neesii* initiated its antheridia in early November, with maturity occurring in mid April. By late July they were all dead. Archegonia, on the other hand, matured only in early May.

Then there are bet hedgers. *Dicranum majus* (Figure 22) in central Norway can form gametangia in late autumn or early spring, permitting fertilization in June and July (Sagmo Solli *et al.* 1998). It appears that this species has not fine-tuned its gametangial timing; mature antheridia are present all summer and autumn, but archegonia are available only in June and July.



Figure 22. Immature sporophytes of *Dicranum majus*. Photo by Michael Lüth, with permission.

The initiation and maturation of sex organs of one sex before those of the other in a population may be a common phenomenon. Longton and Schuster (1983) contend that initiation of antheridia several months before archegonia in dioicous taxa results in their maturation at the same time. In the cases of *Atrichum rhystophyllum* (Figure 23) and *Pogonatum inflexum* in Japan, Imura (1994) found that shoot production of male plants preceded that of females by about four months. Likewise, antheridia production preceded that of archegonia, but antheridia took longer to develop. Similar differences occur in *Atrichum androgynum*, with antheridia beginning development in spring after the sporophytes reach maturity (Biggs and Gibson 2006). Archegonia begin development one month later. Development of the sporophyte takes 12 months, with spores being released in the spring. In four species of *Ptychomitrium* in Japan, Deguchi and Takeda (1986) found that antheridia typically required 9 months whereas archegonia required only 1 month to develop, with both maturing in the June rainy season.

In the functionally dioicous *Pleurozium schreberi* (Figure 13) in Great Britain, perigonia (♂) begin development in August whereas perichaetia (♀) first occur in October (Longton & Greene 1969). Both overwinter and fertilization occurs in April-May. This results in maturation of the sporophyte by October with spores being shed January-April. Fertilization is delayed in more northern areas such as Scandinavia. On the other hand, Greene (1960) found that in *Mnium hornum* (Figure 24) antheridia mature about one month before the archegonia,

perhaps insuring that sperm will be available when proper conditions for fertilization occur.

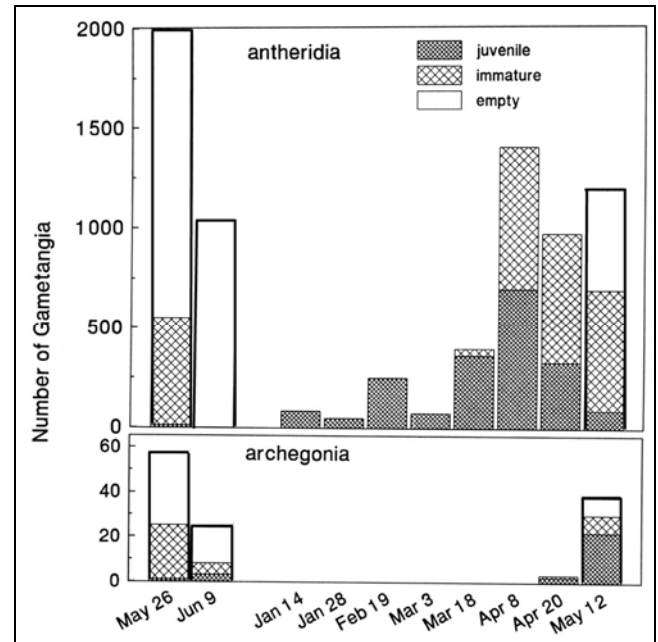


Figure 23. Maturation dates of antheridia and archegonia of *Atrichum rhystophyllum* at Miyajima Island, Japan, during 1987-1988. Samples included 1-10 individuals. Based on table by Imura (1994).



Figure 24. *Mnium hornum* from Europe. Photo by Michael Lüth, with permission.

When differences in initiation time occur, we can presume that different stimuli are needed to initiate the development. This is discussed briefly in the development chapter on gametogenesis, but it appears we know little about the signals for initiation when they differ for the two gametangial types. One such signal is light intensity. In *Riccia discolor*, female clones developed gametangia maximally at 3500 lux continuous light at pH 5.5 (Gupta *et al.* 1991). However, male plants failed to produce antheridia at pH 3.5 or 5.5 at any light intensity in the experiment.

The longer development time for antheridia is common. For example, in Australia *Dicranoloma menziesii* and *D. platycaulon* initiate their antheridia during winter and archegonia in the spring (Milne 2001).

However, the archegonia mature in two months, whereas antheridia require 5-6 months. By contrast, a third species, *D. billardierei* (Figure 25), that is **sympatric** (occurring in the same geographic area) with these two, initiates its antheridia during late spring-summer and its archegonia in autumn. The result is that *D. menziesii* has fertilization in late summer, *D. platycaulon* in mid autumn, and *D. billardierei* in early winter. This separation of fertilization time permits these sympatric species to co-exist without the danger of interbreeding that could soon diminish the species distinctions. The sporophyte development is slow, requiring 18-24 months in *D. billardierei* and *D. platycaulon*, but only 12 months in *D. menziesii*.



Figure 25. *Dicranoloma billardierei*, a species that initiates its antheridia during late spring-summer and its archegonia in autumn. Photo by Michael Lüth, with permission.

Initiation of antheridia before archegonia may extend to monoicous taxa as well. Van der Wijk (1960) reported that 14 out of 18 mosses from the Netherlands initiated antheridia before archegonia; three of these 14 taxa were monoicous. The remaining 4 initiated archegonia in the same month as antheridia; one of these was monoicous. In his study, it was typical for antheridia to be initiated in the autumn with archegonia initiated the following spring. In *Entodon cladorrhizans* (Figure 28), a monoicous perennial, antheridia likewise initiate well before archegonia (Stark 1983).

Antheridia generally require longer to develop than archegonia. Therefore, male and female gametangia must time their development so that they both mature at the same time, and that maturity occurs at a time when water is available for fertilization. That fertilization period typically is less than one month. For many parts of the temperate zone, this means spring is the best season, with autumn being a second possibility, provided early frost is not a danger to the gametes or the embryo. In dry climates and the tropics, winter is usually the best season because of greater moisture.

Protandry and Protogyny

With the advent of the monoicous condition, bryophytes faced the problem of inbreeding. The solution to this is to have a mechanism to prevent that event. When there is no carrier organism involved, this can be

accomplished in two ways. There can be some self-incompatibility mechanism involved, or the two types of gametangia can mature at different times.

Towle (1905) found protogynous timing in *Atrichum undulatum* (Figure 26), Egnyomi (1979) in *Octoblepharum albidum*. Longton and Schuster (1983) summarize several studies that indicate that **protandry** (maturation of antheridia before archegonia on same plant) and **protogyny** (maturation of archegonia before antheridia on same plant) are common among monoicous bryophytes, as in *Funaria hygrometrica* (Figure 27) and *Atrichum undulatum* (Figure 26). [*Atrichum undulatum* is functionally dioicous, at least in Michigan, USA, *i.e.*, it does not produce male and female gametangia on the same plant at the same time, but it can, at least in some populations, produce antheridia the first year and archegonia the next (Crum 1976)]. This is similar to the sequential hermaphroditism seen in some animals such as the blue-headed wrasse. Interestingly, Crum (1976) reports that in North America *F. hygrometrica* produces **perigonia** first (housing antheridia), then **perichaetia** (housing archegonia), making them **protandrous**, but Benson-Evans and Brough (1966) report the same species in Great Britain as **protogynous** (having females mature first).

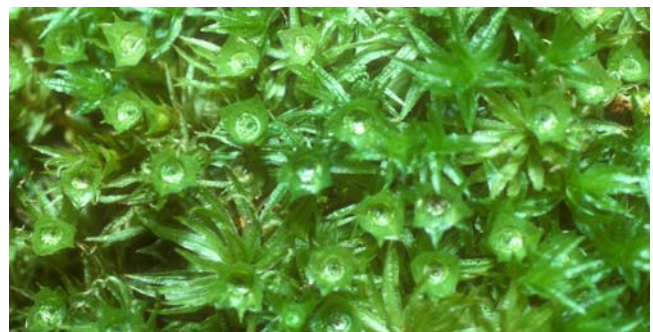


Figure 26. Male plants with splash cups on *Atrichum undulatum*. Photo by Janice Glime.



Figure 27. *Funaria hygrometrica* with young sporophytes in Europe. Photo by Michael Lüth, with permission.

Even in the dioicous perennial moss *Forsstroemia trichomitria*, gametangial maturation is protogynous (Stark 1985). On the other hand, Greene (1960) was surprised to find that in perennial moss *Brachythecium rutabulum* (Figure 10) the intermixed archegonia and antheridia also had intermixed developmental stages for both gametangia,

and that they both appeared to be produced year-round. But in *Bryum argenteum*, although archegonia and antheridia are produced at the same time in Reading, England, in north Wales antheridia typically begin development in November and archegonia in the following April (Miles *et al.* 1989).

Some monoicous mosses may benefit, or at least survive, with self-fertilization. In the Chihuahuan Desert, on *Trichostomum perligulatum* each branch produces an average of 2 archegonia and 3 perigonia containing 6 antheridia, being at first protogynous, but then synchronous, and finally only male. Stark and Castetter (1995) found that fertilization among the gametangia on a single stem in this species appeared to be common.

Sporophyte Maturation

Degree of maturity of sporophytes may be reported in various ways, and the system of Greene (1960; see previous subchapter on phenology) seeks to straighten out these ambiguities. Some authors report the season for spores, which we may assume is the OF (operculum fallen) stage of Greene. Conard (1947), in his phenological study on Iowa herbarium specimens, considered the "perfect capsule" stage to include some opercula shed and others in place. The spike stage of Conard corresponds to the ECI (early calyptra intact) stage of Greene.

Energy Needs

Sporophytes require tremendous energy to mature. Stark and Stephenson (1983) have demonstrated the compensation for insufficient energy in the pleurocarpous *Entodon cladorrhizans* (Figure 28) through abortion of sporophytes, much like the abortion of fruits in *Asclepias* (milkweed). But it would seem that the best way to provide sufficient energy would be to optimize time of development of the sporophyte. To this end, we will examine the timing of capsule production in several examples.



Figure 28. Gametophytes of the monoicous perennial *Entodon cladorrhizans*. Photo by Janice Glime.

A common way to optimize energy is to avoid having two means of propagation at the same time. Thus, *Tetraphis pellucida* produces capsules in spring, whereas gemmae with gemma cups are produced after spores are shed. In *Atrichum undulatum* (Figure 1), spores are shed in March in Vermont (Figure 1), and new archegonia are present by early May (Towle 1905). As already noted, the

antheridia were present earlier (mid April), but they do not compete for sporophyte energy in this dioicous species.

Optimizing Dispersal Time

Often, maturation of capsules is timed to take advantage of dry weather for dispersal. For example, in Nigerian populations of *Octoblepharum albidum*, capsules develop quickly from August to early December, when spore liberation begins, coinciding with the dry season (Egunyomi 1979). But natural phenomena are rarely so predictable. The difficulty in drawing generalizations about behavior based on either habitat or climate is exemplified by comparing *Pylaisiella polyantha* (Figure 29) to *Hypnum cupressiforme* var. *resupinatum* (Greene 1960), two species that have somewhat similar gross vegetative morphologies. Although both taxa are found on the bark of deciduous trees in the same areas in the British Isles, *H. c.* var. *resupinatum* begins its sexual cycle like *P. polyantha*, with a swollen venter in July-August, but instead of the sporophyte requiring a year (or more), as in *P. polyantha*, it soon completes its capsule development and loses its spores beginning in January. Although *P. polyantha* is monoicous and *H. c.* var. *resupinatum* is dioicous, it is difficult to imagine how this could affect development of the sporophyte. Similar differences occur in *Ulota* in Great Britain (Jones 1946). *Ulota crispa* var. *intermedia* capsules mature in July-August, var. *crispula* in spring (Figure 30), and *U. bruchii* (Figure 31) in winter, suggesting that season of dehiscence may not be critical for these taxa in this particular location.



Figure 29. Dehiscent sporophytes and seta spikes representing two cohorts present at the same time in *Pylaisiella polyantha*. Photo by Michael Lüth, with permission.



Figure 30. *Ulota crispa* growing epiphytically. *Ulota crispa* var. *intermedia* and var. *crispula* have different capsule maturation dates in summer vs spring, respectively. Photo by Janice Glime



Figure 31. *Ulota bruchii*, a species where capsules mature in winter. Photo by Michael Lüth, with permission.

One pattern that seems to emerge is that in many terrestrial bryophytes spore dispersal may be timed for alternating moist and dry conditions. If moss spores do indeed depend on flexes of peristome teeth, then a season in which moisture conditions change from wet to dry frequently would be advantageous. Liverworts seem to be largely timed for the same benefit (Schuster 1966). On the other hand, perhaps the important timing is not dispersal as much as it is germination. Spore germination requires water, and if spores are to germinate immediately before being consumed or losing viability, a season of alternating wet and dry could be an advantage. While this latter explanation may have merit for some taxa, it seems that many bryophyte spores are viable for long periods in quite adverse conditions (van Zanten & Pocs 1981; During and ter Horst 1983; During 1986; van Zanten & Gradstein 1988; van Zanten 1992; During 1997; Frahm 2002).

In *Sphagnum*, if the capsule dries too soon, the spores are not mature and are forced out of the capsule before they are mature (Sundberg 2002). It appeared to be an advantage for these taxa to mature and have early spore dispersal in the drought-sensitive lawn species to avoid the risk of premature drying of the sporophyte during the summer droughts.

In *Marchantia polymorpha*, we have already seen that long days are important for development of the archegoniophore, causing it to reach its maximum height by mid summer when sporangia are mature and warm, dry conditions most likely optimize dispersal of the mature spores (Terui 1981). Thus, this liverwort has to time its gametophyte to carry out the function known for the sporophyte stalk of a moss, necessitating the expression of the trait in the gametophyte instead of the sporophyte generation. In its more tropical relative, *M. chenopoda*, sporophytes mature earlier, in late spring to early summer (Moyá 1992), suggesting that temperature may be a signal.

Spring and Autumn Dispersal

The best overall picture of temperate zone sporophyte phenology seems to be that of Conard (1947) for Iowa, USA, bryophytes. He used herbarium specimens from the State University of Iowa and Grinnell College to determine the number of collections with sporophytes each month. Like gametangia, sporophytes exhibited two seasons of abundance. "Spikes," or setae with no capsule development, were present mostly in March - May and October - November (Figure 32). Capsules matured mostly

May - June or October - November (Figure 32). However, these data lack details of timing, and as noted already, could possibly represent development that continued after the collecting date, and could have contained considerable collecting bias.

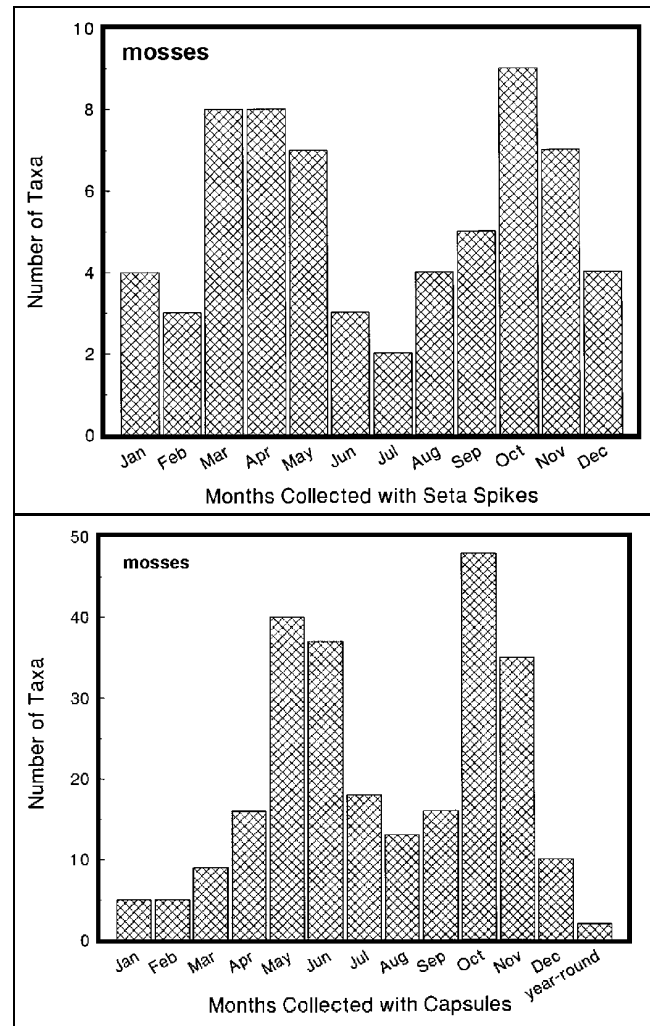


Figure 32. **Top:** Numbers of moss taxa with young setae ("spikes") per month among the 33 taxa that had spikes. **Bottom:** Numbers of taxa per month with capsules. Study based on 232 species of Iowa mosses in the herbaria at State University of Iowa and Grinnell College. Based on table from Conard (1947).

Lackner (1939) showed capsule and spore maturation times of 182 species in East Prussia (now part of Poland and Russia). The capsules are present mostly from May to September, contrasting with the summer low reported by Conard (1947) for Iowa. However, when these taxa are separated into those that do not delay capsule development and those that do, it is the ones that delay development that mature mostly in summer (Table 1; Hughes 1990); the others disperse spores mostly in spring (February - April). Previous work by Arnell (1875), as presented by Lackner (1939), on the beginning of capsule appearances for two locations in Europe are shown in Figure 33 and indicate that the capsules began to form primarily from April to August in those locations. In these same areas and in Germany, Lackner shows spores ripening mostly in May through July, with other peaks (for East Prussia) in February and October (Figure 33).

Table 1. Phenology of (a) 35 species in which capsule formation is not delayed and (b) 42 species in which there is a lengthy delay. Table based on Lackner (1939) and modified from Hughes (1990).

		Number of species making response in each calendar month																				Total number of species	
		J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	
Fertilization	(a)			1	4	12	11	6	1														35
	(b)		1	1	2	11	13	9	4	1													42
Swelling of capsule	(a)							4	16	8	6	1											35
	(b)														4	17	14	7					42
Spore shedding	(a)										1	3	1	12	10	5	2	1					35
	(b)															1	11	13	13	0	4		42
(a)		<i>Hedwigia ciliata</i>										<i>A. subtile</i>										<i>Physcomitrium pyriforme</i>	
		<i>Homalia trichomanoides</i>										<i>Aulacomnium palustre</i>										<i>Plagiomnium affine</i>	
<i>Anomodon viticulosus</i>		<i>Homalothecium lutescens</i>										<i>Bartramia ithyphylla</i>										<i>P. cuspidatum</i>	
<i>Atrichum undulatum</i>		<i>Hylocomium splendens</i>										<i>Bryum caespitium</i>										<i>P. medium</i>	
<i>Barbula unguiculata</i>		<i>Hypnum cupressiforme</i>										<i>B. pallens</i>										<i>P. rostratum</i>	
<i>Brachythecium albicans</i>		<i>Leucodon sciuroides</i>										<i>B. warneum</i>										<i>P. undulatum</i>	
<i>B. populeum</i>		<i>Phascum cuspidatum</i>										<i>Calliergon cordifolium</i>										<i>Plagiothecium cavifolium</i>	
<i>B. rutabulum</i>		<i>Pogonatum urnigerum</i>										<i>Calliergonella cuspidatum</i>										<i>P. curvifolium</i>	
<i>B. velutinum</i>		<i>Racomitrium heterostichum</i>										<i>Ceratodon purpureus</i>										<i>P. nemorale</i>	
<i>Bryum argenteum</i>		<i>Rhizomnium punctatum</i>										<i>Cratoneuron filicinum</i>										<i>Pohlia nutans</i>	
<i>Buxbaumia aphylla</i>		<i>Rhynchostegium murale</i>										<i>Dicranum scoparium</i>										<i>Polytrichum commune</i>	
<i>Climacium dendroides</i>		<i>Rhytidiadelphus squarrosus</i>										<i>Distichium capillaceum</i>										<i>P. formosum</i>	
<i>Dicranella rufescens</i>		<i>R. triquetrus</i>										<i>Encalypta vulgaris</i>										<i>P. juniperinum</i>	
<i>Dicranella</i> sp.		<i>Schistidium apocarpum</i>										<i>Helodium blandowii</i>										<i>P. piliferum</i>	
<i>Didymodon fallax</i>		<i>Tetraphis pellucida</i>										<i>Herzogiella striatella</i>										<i>Sanionia uncinata</i>	
<i>Diselium nudum</i>		<i>Thamnum alopecurum</i>										<i>Homalothecium nitens</i>										<i>Splachnum ampullaceum</i>	
<i>Entodon</i> sp.												<i>Hygrohypnum luridum</i>										<i>Syntrichia ruralis</i>	
<i>Eurhynchium hians</i>												<i>Leptobryum pyriforme</i>										<i>Syntrichia subulata</i>	
<i>E. striatum</i>												<i>Leptodictyum riparium</i>										<i>Tortula muralis</i>	
<i>Fissidens bryoides</i>												<i>Mnium hornum</i>										<i>Warnstorfia fluitans</i>	
<i>F. taxifolius</i>		<i>Amblystegium serpens</i>										<i>M. marginatum</i>											

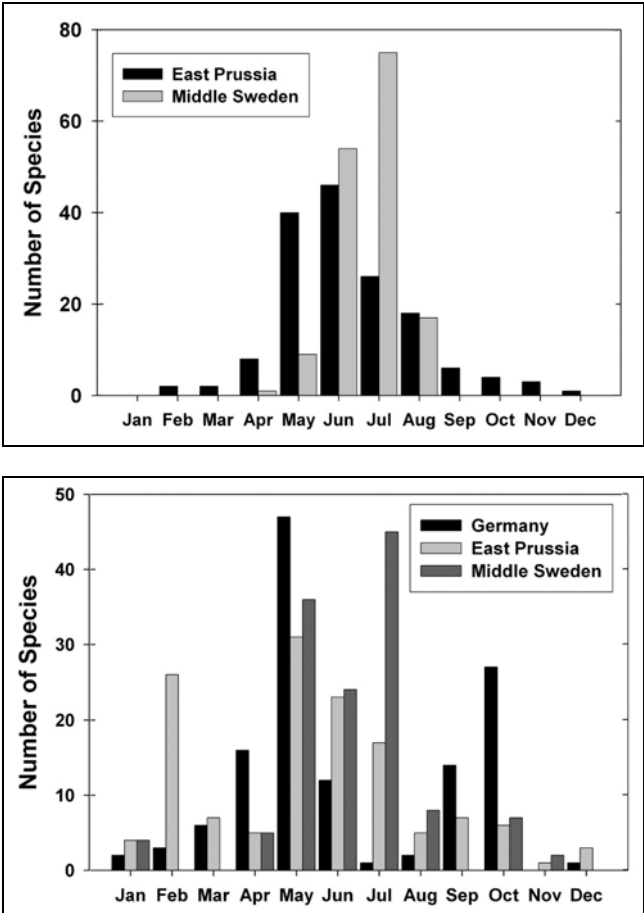


Figure 33. Months of capsule appearance in two locations in Europe. Months of spore ripening in three countries in Europe. Redrawn from Lackner (1939).

As in the mosses, Conard (1947) found that the months with the greatest number of mature liverwort capsules were April - June and September - October. (Figure 34) In a recent study, Bray (pers. comm.) found that the liverwort *Fossombronina foveolata* produces capsules in both spring and autumn on the same individuals, drying out in the summer and surviving by producing a dense terminal bud that seems to be protected by its dark, red-brown color. *Fossombronina* typically lives in places where it gets submerged part of the year and dried out another part, so it is not surprising that it has a life cycle much like some of the moss ephemerals.

In the mild climate of California, USA, the thallose liverwort *Asterella californica* occurs on moist banks and canyon walls, where its growth occurs autumn to spring and its capsules mature in April (Haupt 1929a). It dries out in summer and survives from tips of branches.

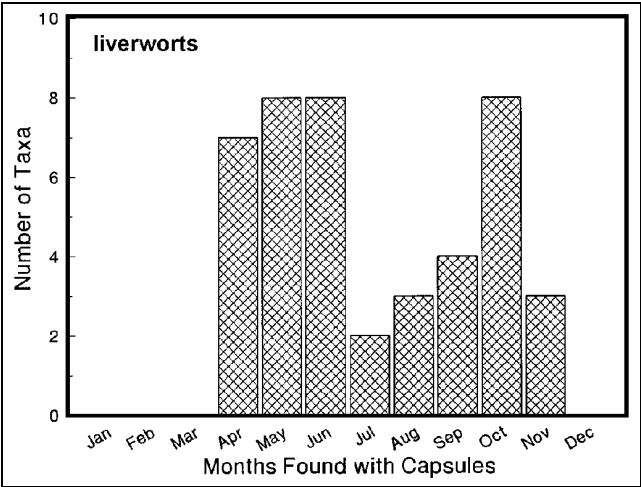


Figure 34. Numbers of liverwort taxa with capsules per month among the 30 taxa having capsules out of 60 Iowa liverwort taxa (including Anthocerotopsida) in the herbaria at State University of Iowa and Grinnell College. Based on table from Conard (1947).

Development Time

Sporophyte maturation can be a slow process, thus crossing multiple seasons. Grimme (1903) reported that in Germany he found the minimum time for sporophyte development to be that of *Atrichum tenellum* (4 months) and the maximum to be for *Grimmia ovata* (24 months). Crum (2001) reports *Polytrichum* to require 13 months and *Dicranum* 17 months. These times differ with geographic location and may depend on such factors as length of growing season, temperature, and water availability. Many other variations occur, attesting to the fact that these sporophytes must withstand a wide range of conditions during their development, yet maintain a timing that is suitable for spore dispersal.

In addition to defining developmental stages, Greene (1960) suggested a scheme based on time required for development (Figure 35).

At least in the temperate zone, the spring and autumn maturation times may follow a long development, as found in *Polytrichum* – 7-16 months in Scandinavia, 9-20 months in Sweden (Arnell 1905), and *Forsstroemia trichomitria* – 17 months (Stark 1984), or 15 months for *P. alpestre* in the Antarctic (Longton 1972). In others, such as *Mnium hornum*, the seta emerges in the autumn, remaining in that state throughout the winter, and continues development in early spring (Greene 1960). In Great Britain, this species has lost its opercula by early May.

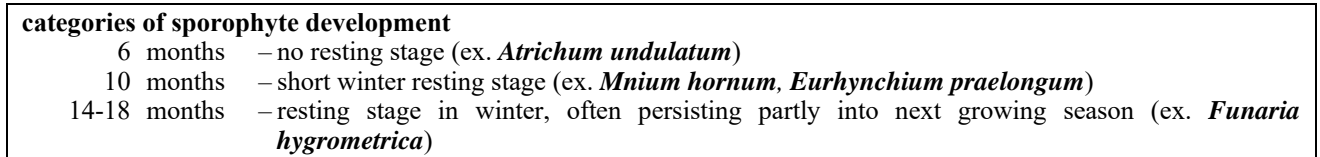


Figure 35. Scheme for representing sporophyte development. Based on Greene 1960; examples from Benson-Evans & Brough 1966.

The capsule cycle of the epiphytic *Pylaisia polyantha* (Figure 29) requires so much time for development that two generations of capsules are present at the same time, not only in Great Britain, but in many locations in both Europe and North America (Greene 1960). The venter is swollen in July to August, and the calyptra is retained for an entire year, falling in the next July. Capsule development continues, with the operculum falling early in the following year. In Great Britain, this species has lost its opercula by early May.

Winter Dispersal

Winter is a good time for capsule maturation to occur in mild climates where that is the moist season. In Great Britain, *Brachythecium rutabulum* (Figure 10) has lost its opercula by early May (Greene 1960). It continues development from its early calyptra stage in September on to an intact operculum with the operculum falling December to February. By March the capsules are empty. If it were to follow that timing in the Keweenaw Peninsula of Michigan, USA, its capsules would be imbedded in snow at the time of dispersal. In Japan, the thallose liverwort *Mannia fragrans* has mature spores in early winter (Furuki 1992).

Lackner (1939) found that *Orthotrichum* species were notable exceptions to the spring and summer dispersals of bryophytes in his study. This epiphytic/saxicolous genus typically produced capsules in the winter months. Perhaps winter is good for mosses if they can avoid being covered by snow, although early frost causes mortality in young capsules of the soil-dwelling *Buxbaumia aphylla* (Hancock & Brassard 1974; Figure 36). The result is that survival depends on the rapid maturation of the sporophyte in the autumn, permitting the capsules to be dormant during the winter.



Figure 36. Young sporophytes of *Buxbaumia aphylla* in Michigan, USA. Photo by Janice Glime.

Winter may also favor aquatic bryophytes, but for somewhat different reasons because the problems are quite different. Dispersal by air would seem to be nearly impossible when the environment is continuously moist or submersed. And, in fact, we have no direct evidence of the success of the spores of such submersed taxa as *Fontinalis*. Nevertheless, *F. novae-angliae* and *F. dalecarlica* produce capsules in winter, at least in New Hampshire, USA, with abrasion apparently serving as the primary means of opening the capsule (pers. obs.). The subsequent dispersal

of the spores is pure conjecture, but since the peristome teeth are generally not exposed to air, one might suppose that water is the only available agent. It is interesting that the aquatic liverwort *Scapania undulata* likewise produces its capsules in winter (Grainger 1947).

Elevation Effects

For those bryophytes not adapted for development during winter conditions, elevation provides evidence of the importance of temperature. For thirteen taxa growing at four elevations in the Eastern Pyrenees, Girona, Spain, those living at higher elevations have dormant sporophytes in the winter, completing their development early in the summer (Lloret 1987). Those that live at lower elevations have continuous development. Only one species among these, *Schistidium apocarpum* var. *confertum*, is able to continue development at locations above 1800 meters.

One of the factors that can affect success of a sporophyte is the weather during development of pre-winter stages, as shown by the high mortality due to early frost in young sporophytes of *Buxbaumia aphylla* in Newfoundland (Hancock & Brassard 1974). In this species, young capsules are formed in the autumn and remain green over the winter, maturing the following spring. By summer, little evidence of the capsule remains, although their thick setae are sometimes still present.

Fortunately, mosses are adaptable in their physiological responses, often resulting in physiological races in different parts of the world. Longton (1979), in comparing *Polytrichum alpestre* populations at the more northern Churchill, Manitoba, Canada, site to those at Pinawa, Manitoba, found that the initiation of the LCP (late calyptra in perichaetium) stage began earlier in the autumn and that shift to the OI (operculum intact) stage occurred later in the spring at Churchill (Figure 37). However, the sporophyte development proceeded more quickly at Churchill during the growing season, surpassing that of the mosses at the Pinawa site, and compensating for the longer dormancy.

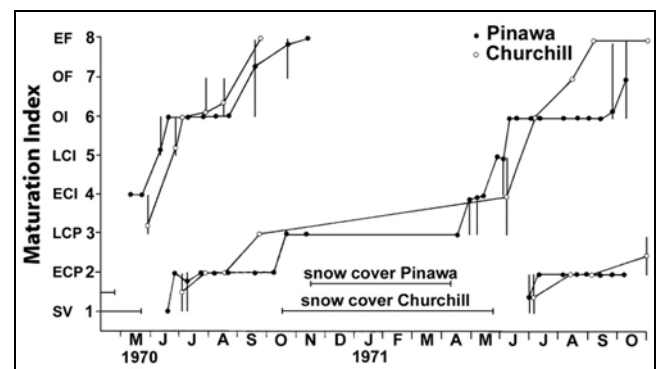


Figure 37. Comparison of sporophyte development of *Polytrichum alpestre* in Pinawa and Churchill, Manitoba, Canada. Points represent the maturity indices with vertical bars indicating the range of stages present. Based on Longton (1979).

Spores and Protonemata

Spore dispersal is most advantageous if the air is dry and breezy, permitting the spores to travel long distances before becoming lodged within the minute crevices of the soil or other substrate. In fact, dryness usually initiates the shedding of the operculum, as illustrated by Johnsen (1969)

for *Orthotrichum anomalum*. On the other hand, to mature, the capsule must have energy available, so these two factors must be included in the dispersal strategy to determine the season of dispersal. It may be this need for energy, then a dry season, followed by a suitable moist season, that some mosses disperse their spores in winter, e.g. *Anomobryum julaceum* and *Bryum argenteum* (Figure 38) (Pedersen & Hedenäs 2002) and the liverwort *Mannia fragrans* in Japan (Furuki 1992). In the seasonally dry interior of North America, *Syrrophodon texanus* has optimal spore release in October to March, followed by rain that peaks in July, then decreases rapidly to a low in November (Reese 1984). As we have already seen, one way to accommodate these needs for energy and the right moisture conditions is for the capsule to persist in a mature state, operculum intact, for months to years before initiating dispersal.



Figure 38. Capsules on *Bryum argenteum*. Photo by Michael Lüth, with permission.

Using herbarium specimens, Nishimura (1993) determined the dates of dispersal for mosses from the Hiruzen Highlands on the island of Honshu, Japan (Figure 39). He found 34 species that disperse spores in late autumn to early spring (late November to early April), 12 in late spring to summer (May to August), and 5 in autumn (September to November). *Bryum argenteum* dispersed in both spring and autumn. *Sematophyllum subhumile* subsp. *japonicum* was the only species that had no definite season of dispersal. Although herbarium specimens can introduce error because opercula tend to come off more easily under the dry conditions of the herbarium, the 551 specimens used in this study give us a general picture of events.

Egunyomi (1979) found that capsules of *Octoblepharum albidum* in Nigeria matured just in time for spores to be liberated during the dry season. Stark (2001a.) finds that most desert bryophytes release spores year-round, an advantage in a dry climate where rainfall is rare and not seasonal. On the other hand, spores in *Pleurozium schreberi* (Figure 13) in Britain are shed January-April when it is cool and relatively moist (Longton & Greene 1969). In a later study in Great Britain, Longton and Miles (1982) found that five mosses had fertilization in the period of April to July, but that sporophyte maturation time varied considerably. Spore liberation took place from six to twelve months later, spanning a variety of climatic conditions.

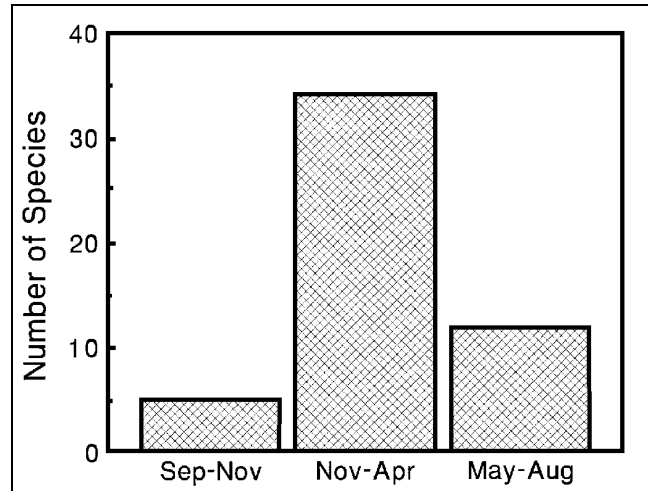


Figure 39. Seasons of dispersal in 51 species of mosses from the Hiruzen Highlands, Honshu, Japan. From data of Nishimura (1993).

To determine the availability of spores, Fenton and Bergeron (2006) studied the spore dispersal of *Sphagnum* species in a black spruce (*Picea mariana*) forest in Québec, Canada. Using spore traps, they determined the phenology of spore dispersal (Figure 40) for two years. Dispersal at these locations began in July, rose in mid August, and ended mid to late September, with peak dispersal near the beginning of September. The earlier dispersal than that of the study in Japan (Nishimura 1993) may be the result of the higher latitude.

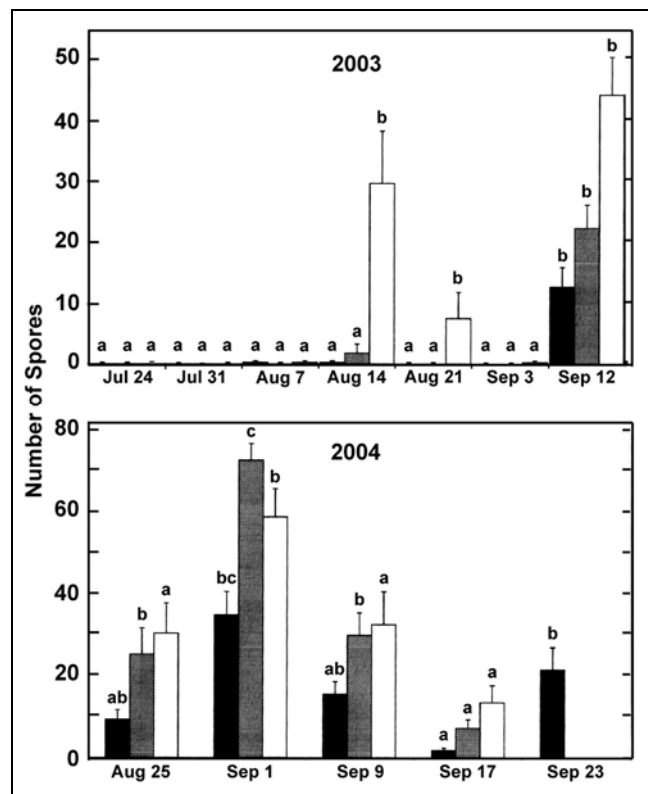


Figure 40. Number of spores collected in 20 spore traps at each of three sites in Québec, Canada. Vertical bars represent standard error. Different letters indicate those values that are significantly different within a site. Redrawn from Fenton & Bergeron (2006).

Although the time of spore dispersal is fairly well known, or at least available in herbaria, virtually nothing is known about the time of spore germination. Longton and Schuster (1983) comment that little is known about spore dormancy in liverworts and virtually nothing about the effect of day length on germination. This is due largely to the difficulty of locating this stage and, even if located, to identify even the genus, much less the species.

We can speculate on the importance of timing for spore establishment. Proctor (2000) pointed out that the need for water would limit the successful establishment of spores and their protonemata on rocks and bark to the lengthy wet season of autumn and winter in western Europe and whatever wet season elsewhere.

Even in taxa with persistent protonemata, *e.g.* *Buxbaumia*, where sexual organs are produced directly on the protonema, field knowledge is lacking. After extensive study of *Buxbaumia aphylla* spanning three years, Hancock and Brassard (1974) were unable to determine if the protonema persisted for more than one season or if the gametangia were produced the same season.

In most taxa, it is probably not necessary to couple suitable germination and protonema development conditions with those of dispersal. Spore viability can last from less than an hour in some epiphyllous and epiphytic liverwort taxa (Longton & Schuster 1983) to 50 years in other bryophytes (Sussman 1965), and probably longer in some taxa. Most spores probably have considerable longevity, as seen in several diaspore bank studies in the Netherlands (*e.g.* During 1986, 1990, During & ter Horst 1983, During *et al.* 1987). They even survive temperatures near absolute zero when dried and placed in vacuum tubes (Becquerel 1932). Van Zanten (1976) has shown that most taxa can survive desiccation for one year, with wet-frozen spores surviving better than dry-frozen ones. But for spores that fall near their parents and do not effect long-distance dispersal, immediate germination success will provide a better chance of establishing the next generation, particularly in overwintering annual taxa, by giving them an early start and a higher percentage of survival.

Protonemata can likewise survive considerable drying (Lipman 1936) and in some taxa such as *Grimmia* may even require a drought period before advancing to the next stage (During, pers. comm.). In fact, Johnsen (1969) found that in *Orthotrichum anomalum* watering during the dormant period (hot and dry) was detrimental. Thus it appears that germination should require more than just the right seasonal event, but rather a seasonal event coupled with the right environmental conditions to take things to the next stage. There seems to be no hope at present of generalizing about phenological events related to the protonemata based on any foundation in data.

Duration of Stages

Longton (1997, 1998) found that those bryophytes that have shorter life spans become reproductively active at a younger age and tend to have greater phenological flexibility. This strategy necessarily implies that each stage is short. This is especially true for the colonists, fugitives, and annual shuttle species to be discussed later in the life strategies chapter. For those taxa that stay longer, the stages may be longer, often depending on habitat characteristics, particularly availability of water.

Gametangia

One of the factors that is important in maintaining distinct species when more than one member of a genus cohabit a region is that their reproductive periods do not overlap or that their means of dispersing gametes are mutually exclusive. Among three Australian species of *Dicranoloma*, all three species studied required 5-6 months for antheridia to mature, but only 2 for archegonia (Milne 2001), the longer time for antheridial development being typical for most mosses. Yet the timing for these three taxa was such that their periods of fertilization were mutually exclusive.

For *Entodon cladorrhizans* (Figure 28) growing in Pennsylvania, USA, the fertilization period lasts five weeks (Stark 1983). In the desert moss *Syntrichia inermis* (Figure 41), maturation of the antheridia takes one to several years due to the intervening dry periods that cause dormancy (Stark 1997).

Table 2 provides additional examples of maturation times, ranging from less than one month for some archegonia and three months for some antheridia to nearly one year for others.

Sporophytes

Ephemeral species have short-lived capsules that may last only a few weeks. Liverworts do likewise, with their deliquescent stalk soon withering away. Furthermore, the valvate capsules of liverworts shed all the spores at one time, whereas in mosses peristome teeth operate to extend dispersal over a longer period, providing the mosses with more opportunities to disperse under conditions favorable for greater dispersal or germination success. *Sphagnum* likewise has short-lived stalks, in this case a deliquescent pseudopodium that develops from the gametophyte to extend the capsule away from the plant. It lacks teeth and disperses most of its spores in one explosive burst when the operculum is shed due to capsule drying and at least some of the time, internal gas expansion due to high temperatures.



Figure 41. *Syntrichia inermis* in its dry state beneath shrubs. Photo courtesy of Lloyd Stark.

But other mosses may have quite extensive periods of sporophyte development. In *Dicranoloma*, *D. billardierei* and *D. platycaulon* required 18-24 months while those of *D. menziesii* required only 12 (Milne 2001). *Atrichum androgynum* likewise requires 12 months for sporophyte maturation (Biggs & Gibson 2006).

Table 2. Examples of times of initialization of gametangia, fertilization, and spore dispersal in bryophytes in the temperate zone.

	location	antheridia initialized	archegonia initialized	fertilization	spores dispersed	reference
<i>Atrichum undulatum</i>	UK	Jan-Feb	Apr-May	May-Jun	Jan-May	Miles <i>et al.</i> 1989
<i>Polytrichum juniperinum</i> (= <i>P. alpestre</i>)	UK	Sep-Oct	Mar-Apr	Jun	Jun-Jul	Miles <i>et al.</i> 1989
<i>Bryum argenteum</i>	UK	Oct-Nov	Apr-Jun	Apr-Jun?	Jan-May	Miles <i>et al.</i> 1989
<i>Grimmia pulvinata</i>	UK	most of yr	most of yr	most of yr	Apr-Jun	Miles <i>et al.</i> 1989
<i>Tortula muralis</i>	UK	anytime	anytime	anytime	Apr-Jun	Miles <i>et al.</i> 1989
<i>Pellia epiphylla</i>	UK	Jan-Jun	Jun	Jun	Mar-Jun	Clapham & Oldroyd 1936
<i>Cephalozia</i>	UK	Feb	Mar	May	?	Clapham & Oldroyd 1936
<i>Marchantia polymorpha</i>	UK	Mar-Apr	Mar-Apr	May	Aug	Clapham & Oldroyd 1936
<i>Aplozia</i>	UK	Apr	May	Jun	May	Clapham & Oldroyd 1936
<i>Conocephalum conicum</i>	UK	Apr-Jun	Jun-Jul	Jul	Mar-Apr	Clapham & Oldroyd 1936
<i>Conocephalum conicum</i>	MI, USA	Aug	Aug	Jun	Apr	Taylor & Hollensen 1984
<i>Diplophyllum</i>	UK	Dec	Jan	May	May	Clapham & Oldroyd 1936
<i>Scapania</i>	UK	Dec	Jan	May	May	Clapham & Oldroyd 1936

Mosses that depend on rainy periods may have very short periods for maturation of the sporophyte, attuned to dispersal at the end of the rainy season, as in *Racomitrium africanum*, *Fissidens glauculus*, *Thuidium gratum*, and *Stereophyllum* sp. from SW Nigeria (Odu 1981). These mosses required 12 months from onset of gametangia to capsule maturity and dispersal, but sporophyte development itself is complete at the end of the rainy season (October-December), following gametangial development at the onset of the rainy season (March/April). Spore dispersal occurs during the dry season (November-April). The entire process requires 12 months. Other desert mosses can have very long maturation periods spanning several years with long dormancy periods intervening.

The soil-dwelling *Syntrichia inermis*, in the Mojave Desert, USA, requires about 21 months for sporophyte development, while being dormant for 18 of those months (Stark 1997). Span of operculum detachment may last up to 2.5 years, and capsules of the same cohort may disperse spores over a period of three years (Stark 2001a). In the same desert, the rock-dwelling *Grimmia orbicularis* required only 3 months for its capsule to mature following meiosis, and its operculum dehiscence spanned only three weeks; spore release of the cohort lasted about six months (Stark 2001a).

The perennial moss *Entodon cladorrhizans* (Figure 28) requires six to nine months for the sporophyte to mature (Stark 1983).

Zander (1979) did an exhaustive study in the Pottiaceae of the north temperate zone of Europe, Asia, and North America, comparing dioicous and monoicous taxa. The Pottiaceae typically require 12-13 months for sporophyte development (Krieger 1915), but Zander found that the phenology of the two sexual conditions differed, with dioicous taxa having mature capsules over a slightly longer period of time than did monoicous taxa. Non-endemic dioicous taxa have a mean span of mature capsules of 6.77 months, whereas the non-endemic monoicous ones have only a 5.55-month mean. Among the 86 dioicous taxa studied, 12 have mature capsules spanning nine or more months, whereas only 5 of the 82 monoicous taxa exhibit this duration. He reasoned that this afforded dioicous taxa a better chance for dispersal, perhaps in part compensating for the smaller likelihood of fertilization.

This compensation concept was further supported by finding that the monoicous taxa did not have a significantly wider distribution. Since the ratio of monoicous to dioicous taxa in Pottiaceae is similar to that of bryophytes as a whole, this study might be a model of mature capsule duration in monoicous vs. dioicous taxa. It would be interesting to determine if capsule duration can indeed compensate for the reputedly greater percent of species producing capsules among the monoicous taxa than among the dioicous ones (Gemmell 1950, Longton & Schuster 1983).

Winter Effects

In bryophytes, unlike the tracheophytes, embryos and gametangia are capable of surviving prolonged freezing of winter (Stark 1984). Continuous melt of snow during parts of the winter could facilitate fertilization of some bryophytes under the snow, but no broad-scale studies have examined this in areas where the phenomenon is likely, and while the gametangia might survive, one must question whether the sperm can swim and locate a female at near-freezing temperatures. Furthermore, while sperm can swim at speeds of 100-200 μm per second (Richards 1978), they require a chemical attractant to find the archegonium (Muggoch & Walton 1942), and cold temperatures might reduce the effectiveness of such an attractant. Even so, we know that the aquatic liverwort *Scapania undulata* produces gametangia and accomplishes fertilization in winter (Grainger 1947).

On the other hand, Imura and Iwatsuki (1989) found that in *Trachycystis microphylla* (Figure 42) in Japan, antheridia production begins in January with sperm being released March to May. Archegonia production is delayed until March, but they are ready to accept sperm from April to July. The partitioning of energy among life cycle stages would appear to be complex in this species, with overlapping life cycle stages, since spores are released near the time of fertilization of the next generation. (Imagine sending one kid off to college while you are pregnant with the next!) Development of the sporophyte begins in May, and rapid sporophyte elongation occurs in October to November and again in February. Spores are released in April – apparently near the time sperm are released. One would think this delicate timing would require competing

environmental conditions, wet for sperm and dry for spores. Since spring is a time of alternating sunshine and rain, these contrasting conditions are probably available.



Figure 42. *Trachycystis microphylla*. Photo by Li Zhang, with permission.

One explanation for the success of overwintering antheridia as a strategy is that it may spread out the energy requirements over a longer period and give antheridia a chance to grow rapidly in spring, thus insuring that they precede the archegonia in maturity. Benson-Evans and Brough (1966) found that a cold period followed by warmer temperatures can induce more rapid maturation of sex organs if sufficient moisture is available, whereas low temperatures and drought retard development. In this case, the antheridia would receive the stimulation, but the archegonia, by delaying initiation until spring, would not. This advantage is consistent with the 10 out of 18 taxa examined by van der Wijk (1960) in which male gametangia overwintered; female gametangia in these were generally initiated in early spring. One must ask why it is the males that seem to overwinter, whereas females of the same species often delay initiating gametangia until spring. Is it because winter is in fact destructive, but male gametes are much more abundant than are female gametes and can therefore afford to sacrifice some in order to mature earlier? Is there some developmental reason why antheridia require a longer time to develop than do archegonia? Or is it a mechanism to increase protandry, thus ensuring at least some cross fertilization?

Despite the ability of gametangia to survive over winter, Arnell (1905) reported that most of the 33 German and Swedish taxa he studied had gametangial dehiscence in the summer, which suggests that fertilization must have occurred then as well. However, many parts of the world lack sufficient moisture in summer to ensure fertilization.

Huneck *et al.* (1984) determined that essential oils in the temperate leafy liverwort *Bazzania trilobata* were highest in September and lowest in January, suggesting that perhaps these oils might be used for energy reserves during autumn and early winter. It is also possible that they offer a protective function to the cells during the period of freezing and thawing in autumn.

Geographical Differences within Species

Earlier studies by Richards (1959) indicate that seasonal behavior of bryophytes may vary in different climatic regions. The basic developmental pattern of gametangia and sporophytes may differ. Furthermore, lack of proper environmental signals, such as not reaching the

necessary temperature at the necessary photoperiod, or inability of the plant to interpret the signals, can result in failure to produce gametangia or in failure of females to produce mature archegonia at a time when sperm are ready for release (Newton 1971, 1972, Longton 1972).

Even within a small geographic range, signals can come at a different time. For example, in North Wales, *Bryum argenteum* begins development of antheridia before winter, in November, whereas archegonia develop in April (Miles & Longton 1987). In Reading, UK, both gametangia develop at the same time.

Some taxa have adopted different physiological responses in different parts of the world, as, for example, *Lunularia cruciata* (Figure 43), which seems to function as a long-day plant in Wales and a short-day plant in Israel (Longton 1974), but in much of the British Isles it is the climate that prevents this liverwort from producing an archegoniophore and capsules (Benson-Evans & Hughes 1955).



Figure 43. *Lunularia cruciata*, a long-day plant in Wales but a short-day plant in Israel. Photo by David Holyoak, with permission.

Elevation has a strong effect on timing of the life cycle in the Eastern Pyrenees. Bryophytes at high elevations have arrested sporophyte development in the winter, with maturation occurring in the summer concurrent with the next fertilization. However, at lower elevations, there is a continuous progression of stages with no dormant period. *Schistidium apocarpum* var. *confertum*, however, lives at elevations above 1800 m but, like lowland taxa, has no dormant period in winter.

The example of *Funaria hygrometrica* (Figure 27), as studied by Hoffman (1966), exemplifies the sorts of controls that determine the selection pressures affecting the maturation cycle. In that moss, Hoffman found that gametophytes appeared in early spring, with sporophytes maturing in June, but that maturation dates were progressively later at higher elevations. High light intensities contributed to more rapid gametophyte development, while a longer photoperiod resulted in larger stems and leaves. Thus, physiological controls adapt the bryophytes to their particular conditions and may be important factors in selection as bryophytes spread around the world. Whereas morphological variation between species is limited by small size, it is possible that bryophytes may have greater physiological variability than do tracheophytes, enabling individual species to occupy

wider ranges of conditions than those of their tracheophyte counterparts. These adaptations permit bryophytes to conserve energy and to optimize it across time.

Seasonal Differences among Habitats

It is the sum total of the timing of all the life cycle stages that can adapt a bryophyte for a better rate of survival. As the seasons change, so do the selection pressures. Hence, we find that sperm dispersal is timed to coincide with a rainy season and spore dispersal with dry air. But these timing events differ considerably among habitats because the advantages of seasons vary among habitats.

Temperature, length of growing season, available moisture, and photoperiod all have effects on phenology. Studies on elevation can give us clues as to the effects of temperature, although gradients of these other variables exist as well. As already discussed, at low elevations of the Eastern Pyrenees, Spain, the life cycles follow a continuous progression of events with no dormant season (Lloret Maya 1987). By contrast, those living at higher elevations exhibit mature gametangia and accomplish fertilization in the first months of summer, with the sporophyte overwintering in a dormant state and maturing rapidly in early summer. If such differences exist in response to altitude, we might expect even greater differences among habitats of highly contrasting conditions. We shall examine the contrasts among the tropics, deserts, disturbed habitats, and wetlands as representatives of this spectrum.

Tropics

The rainy season is the primary governing factor in the phenology of many tropical mosses (Odu 1981). In four very different taxa of mosses [*Racopilum africanum* (Figure 44), *Fissidens glauculus*, *Thuidium gratum*, and *Stereophyllum* sp. (Figure 45)], Odu found that gametangia develop at the onset of the rainy season (March/April), sporophytes develop later (October – December), and sporophyte maturation occurs at the end of the rainy season. In *F. glauculus* and *T. gratum*, sporophytes developed immediately after fertilization, and within one month in *R. africanum*, with all three producing mature capsules by the end of the rainy season (Odu 1982). Dispersal in these taxa begins at the end of the rainy season and continues into the dry season (November to April) (Odu 1981).



Figure 44. *Racopilum africanum* with young sporophytes. In this species, gametangia develop at the onset of the rainy season and the sporophytes mature at the end of it. Photo by Jan-Peter Frahm, with permission.



Figure 45. *Stereophyllum radiculosum*, one of the mosses where gametangia develop at the onset of the rainy season and the sporophytes mature at the end of it. Photo from Missouri Botanical Garden, with permission.

This same seasonal pattern existed in the herbarium specimens Odu examined (Odu 1982). The rainy season is likewise the best season for development of juveniles and gametangia for *Octoblepharum albidum* (Figure 46; Pôrto & Oliveira 2002). The importance of humidity for *O. albidum* is underscored by its development of sporophytes one month earlier at sites in western Nigeria, with constantly high humidity, than at sites with lower humidity (Egunyomi 1979). Thus, gametangial timing must be set so that capsule maturation is completed in time to take advantage of dispersal in the dry season. Hence, archegonia mature during the rainy season and sporophytes begin developing while it is still rainy. It appears that these tropical bryophytes differ from temperate bryophytes in that their rapid cycle permits them to disperse spores during the next dry season and germinate when the rainy season returns.



Figure 46. *Octoblepharum albidum* on tree bark in Florida, USA. Photo by Janice Glime.

Initiation of archegonia and antheridia in some tropical taxa may occur throughout the year, as it does with *Sematophyllum subpinatum* (Figure 47), nevertheless increasing in frequency during the rainy season (de Oliveira & Pôrto 2001). Although the most favorable season for fertilization is during the rainy season, it likewise can occur throughout the year in that species. Sporophyte development of *S. subpinatum* usually begins later in the rainy season, reflecting the higher fertilization rates during that season.



Figure 47. *Sematophyllum subpinnatum*, a moss that produces antheridia and archegonia throughout the year, from the Neotropics. Photo by Michael Lüth, with permission.



Figure 49. Rock-dwelling *Grimmia orbicularis*. Photo by Michael Lüth, with permission.

Deserts and Dry Habitats

Growth in winter is most likely typical in the desert. Stark (2001a, 2002c) suggests that phenology of bryophytes of the Mojave Desert, USA (Figure 48), contrasts sharply with that of other climatic regions, such as Nigerian savannah mosses, with phenological events tied almost solely to local rainfall events, which are rare and unpredictable. One adaptation to this unpredictable environment is that spore dispersal occurs over a long period. *Grimmia orbicularis* (Figure 49-Figure 50), a rock-dwelling species, retains operculate capsules for three months before its 3-week dispersal period (Stark 2001a). The entire clone, however, may disperse spores over a period as long as six months and within the area may last more than one year. This long dispersal period may also partially compensate for the very high rate of sporophyte abortion in these mosses following a summer rainfall that apparently uses up too many resources in repairing the cells (Stark 2001b). *Syntrichia inermis* (Figure 51), a soil-dwelling species, retains operculate capsules for eleven months, then disperses spores for up to 2.5 years, the clone dispersal lasting up to 3 years! Stark (2001a) concluded that the steeply inclined rock surfaces, supporting short, broad, inclined capsules, account for the more rapid rate of operculum shedding in *Grimmia orbicularis* (Figure 50).



Figure 48. Mojave Desert where *Syntrichia inermis* survives under shrubs and may be dormant for long periods. Photo courtesy of Lloyd Stark.



Figure 50. Capsule of *Grimmia orbicularis*. Photo by Michael Lüth, with permission.

But one can learn a lot about what makes things work by stressing them to their limits. Deserts provide a good model for such stressful conditions. Stark (2002b) found that in the Mojave Desert, one population of *Syntrichia inermis* (Figure 51) initiated sporophyte development in 1995, but that the cohort remained dormant until early 1998. By that time, approximately 66% of the sporophytes had aborted. The remaining viable sporophytes of this group were considerably shorter and had less biomass than the previous cohort. In the next two years, sexual reproduction failed completely, apparently due to reduced winter-spring rainfall. On the other hand, it appeared to be heavy summer rainfall in 1997 that caused the abortion of many of the 1995 sporophyte cohort, with sporophyte numbers increasing again following 1998 summer rains. Stark suggested that the abortion may have been the result of rapid drying and high temperatures while the sporophytes were hydrated, causing membrane damage.

In dry habitats such as the desert, it is often easier to eke out a tiny bit of water in the winter than in the summer when the little rain that does fall evaporates almost before it lands. Hence, we should expect the phenology of desert bryophytes to be different from that of bryophytes in most other habitats. Mojave Desert populations of *Syntrichia inermis* (Figure 51) took an incredibly long time for

antheridia to mature (Stark 2001a). Whereas the archegonia matured and became receptive in the same year, antheridia took one to several years to develop! Despite this long maturation time in which desiccation was a common state, the abortion rate was only 3-4% for either gametangium type. Not surprisingly, more than 90% of the plants were morphologically bisexual. And unlike their temperate and northern counterparts, their growth was in the winter, albeit only 1.4 mm per year. To take advantage of this cooler and more moist season, fertilization occurred in winter, and despite the frequent desiccation, 50% of the perichaetia bore embryos. These embryos remained dormant from spring until fall, resuming their growth once more in the cooler days of winter when the seta and capsule developed (Stark 2001a); sporophytes endure 18 or more months of dormancy during their development (Stark 1997). Spore dispersal, however, was delayed until late summer and early fall.



Figure 51. *Syntrichia inermis* with capsules in various stages of dispersal. Photo by Michael Lüth, with permission.

Syntrichia inermis (Figure 51) sets several bryophyte records through its phenological strategies to survive in the desert (Stark 1997). Considering the importance of reproductive development during the unpredictable and rare rainy periods, it is not surprising that it has the lowest known rates of stem elongation. It also has the longest known period required for antheridial maturation. Growth is greatly sacrificed to complete reproduction, presumably permitting the spores to remain dormant for long periods of time and to disperse over a wide range.

Syntrichia caninervis (Figure 52) also a resident of the Mojave desert, exhibits a sex ratio of roughly 7.9 female to 1 male to 3.1 non-expressing individuals (Stark *et al.* 2001). This large ratio of female to male may help to compensate for the 63% loss of developing sporophytes observed during three years of study. However, there is also partial, if not complete, compensation of sexes by the greater number of reproductive units on males than on females.

Herrnstadt and Kidron (2005) examined reproduction in *Bryum dunense* in three different habitats in the Negev Desert, southern Israel. Despite differences in exposure, including exposed site, under shrub canopy, and partially shaded at foot of north-facing dune slope, all three populations initiated their gametangial development prior to the first winter precipitation. This suggests that the

species are attuned to their environment by a signal such as declining day length or temperature. This prepared them for dispersal of both bulbils and sperm as soon as water was available.

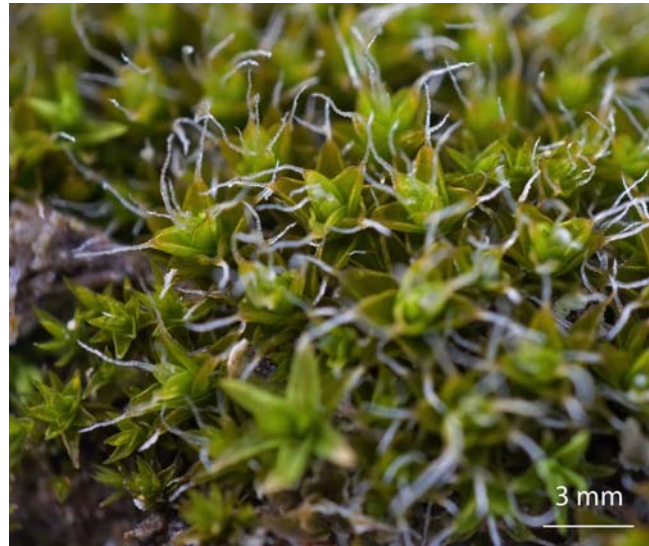


Figure 52. *Syntrichia caninervis*. Photo from Proyecto Musgo, through Creative Commons.

In the dry mountains of southern New Mexico, USA, a close relative of several desert species, *Syntrichia ruralis* (Figure 53) grew, in this case by **innovations** (new shoots), in midwinter (Mishler & Oliver 1991). Female gametangia likewise were initiated in midwinter, causing cessation of growth in that innovation – a definite tradeoff. These female gametangia remained on the plants 6-9 months (December to Jun or even until August), during which no male gametangia were evident, and, of course, no sporophytes. But growth and structural development do not tell the whole story. In this species, the chlorophyll to dry weight ratio was higher in the late summer and winter than it was in early summer. One must pause to wonder what circumstance permitted the higher late summer values.



Figure 53. *Syntrichia ruralis* var. *ruraliformis* (Sand-hill Screw-moss). Photo by Barry Stewart, with permission.

When maturation of gametangia is an autumn event, it forces the young embryo to survive the winter. Haupt (1929b) found that the liverwort *Fossombronia longiseta* in California, USA, had gametangia in the "best" condition

in November and December, perhaps relating to the wetter weather in winter. The overriding importance of water is evidenced by *Octoblepharum albidum* in Nigeria, where immature antheridia and archegonia are most abundant during July, the wettest month (Egunyomi 1979).

Moisture obviously is important in the regulation of season of growth. In the mountains of southern California, *Asterella californica* (Figure 54) grows on canyon sides and moist banks that become dry in summer. The liverwort dries out in summer (cf. Figure 55), surviving by terminal buds (Haupt 1929a). Bray (pers. comm.) found a similar survival mechanism in *Fossombronina* (Figure 56) in southern Illinois, permitting it to grow in fall through spring.



Figure 54. *Asterella californica*, a liverwort that dries out in summer and survives by terminal buds. Photo by Peter J. Bryant, University of California, Irvine, with permission.



Figure 55. *Asterella tenella* with drying thallus and mature archegoniophore with open capsules. Photo by Janice Glime.

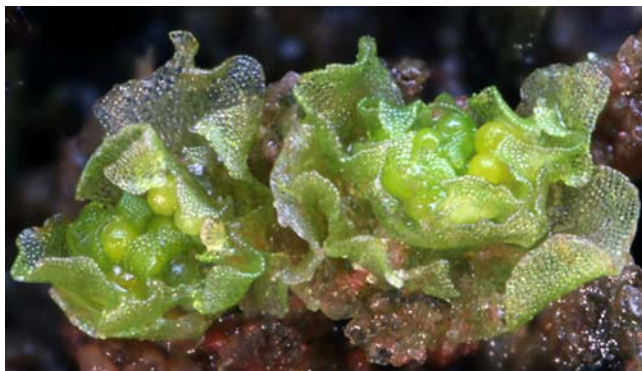


Figure 56. *Fossombronina incurva*. Photo by Des Callaghan, with permission.

Trichostomum perligulatum, a tiny **protogynous** (producing female organs before male organs) desert moss, has populations 20-50 years old (Stark & Castetter 1995). It solves the capsule drying problem by having fertilization in late fall with sporophytes maturing continuously until spring, when it disperses its spores. Completion of its entire sexual cycle during cooler months, coupled with extensive intra-stem fertilization, permits it to survive its desert habitat.

Bryophytes in deserts are very dependent on the annual moisture cycle for their life cycle. In the Nigerian desert, sexual cycles are short, occurring completely within the rainy season. In the Mojave Desert in southwestern USA, there is no rainy season, and rainfall events are unpredictable. In that regime, bryophytes have very long sexual cycles, sometimes taking several years to develop antheridia, several years for capsules to mature, and six months to disperse all the spores. Growth is mostly in winter, fertilization is in winter, and dispersal of spores occurs in late summer and early autumn. Some dry habitat thallose liverworts become dormant in summer, surviving as terminal buds while the remaining thallus dies.

Epiphytes

Epiphytes live in a habitat that is frequently dry, but unlike the desert, water is also frequently available. This alternate wet-dry microclimate brings its own set of problems. There can be relatively long periods of time when it is unsuitable for sperm transfer. The epiphyte *Forsstroemia trichomitria* (Figure 57) produces five sets of reproductive structures per year. This may be an adaptation to increase the chances of having the right weather (rain) to accomplish fertilization. Fertilization occurs in late summer through autumn, about four months duration. Both types of gametangia are produced at the same time. The sporophytes require 17 months for maturation, enduring two winters.



Figure 57. *Forsstroemia trichomitria*, an epiphytic moss that produces five sets of gametangia each growing season. Photo by Misha Ignatov, with permission.

Savannah

Contrasting with mosses controlled by the rainy season, as in the tropics, or those of dry periods that can last years, mosses of the dry habitat of Nigerian savannah

have much shorter sexual cycles than those of the desert, as noted by Makinde and Odu (1994) for four mosses, *Archidium ohioense* (Figure 58), *Bryum coronatum* (Figure 59), *Fissidens minutifolius* (Figure 60), and *Trachycarpidium tisserantii*. Their entire sexual cycle, from production of gametangia to dehiscence of capsules, occurs during the rainy season. Protonemata and gametophytes develop in March-April; capsules mature and spores are dispersed in September-October. Nevertheless, spore discharge is somewhat difficult in the **cleistocarpous** *A. ohioense* and *T. tisserantii* compared to the other two species. (Cleistocarpous capsules have no operculum and must break apart without aid of lines of dehiscence to expel their spores.) Makinde and Odu suggest that this short maturation period may be advantageous in their savannah habitat.



Figure 58. *Archidium ohioense*. Photo by Li Zhang, with permission.



Figure 59. *Bryum coronatum* in India, a moss that completes its entire sexual cycle during the rainy season in the savannahs of Nigeria. Photo by Michael Lüth, with permission.



Figure 60. *Fissidens minutulus*, a generic relative of *F. minutifolius* – one of the mosses that completes its entire sexual cycle in the rainy season in the savannahs of Georgia. Photo by Jan-Peter Frahm, with permission.

Polar and Alpine

Ayukawa *et al.* (2002) investigated *Polytrichum ohioense* in the Yatsugatake Mountains of Japan. They found mature antheridia from late May to early August and mature archegonia from late June to mid July, permitting fertilization to occur from late June to mid July. This timing of gametangial maturity avoided the occasional temperatures below 0°C in May. The longer period of sperm maturity permits variability in time of egg maturation and suggests that the two types of gametangia respond to different triggers. Sporophytes began showing at the end of June, became dormant for the inter, and began growth again in May. Spores were dispersed from mid July to mid August. Hence the 13-month sporophyte maturation included a 6-month resting period in winter.

Antarctic populations of *Polytrichum juniperinum* (as *P. alpestre*) behave quite differently (Longton & Greene 1967). The antheridia begin development in March and overwinter (May-October) with no further development. Development resumes after snowmelt and most of the antheridia mature in December-early January. Archegonia, on the other hand, do not begin development until the end of November, but still reach maturity at the same time as the antheridia. Sporophyte development was much longer, beginning with fertilization in December and January but not completing development until mid-March the following year.

Clarke and Greene (1970) found somewhat different timing adaptations in populations of *Pohlia* in the Arctic and sub-Arctic. In these populations, maturation was somewhat faster than for the same species in Britain.

Disturbed Habitats – Ephemerals

The ephemerals, or short-lived taxa, face some of the same problems as desert bryophytes. They are very dependent on climatological events to coordinate their phenological events. They often grow in areas that experience flooding during part of the year. Although the sequence of most life cycle events is poorly known in ephemerals, Crum (1976) provides us with information on when to expect to see these plants (capsules) in Michigan. We can suppose that during the remainder of the year the moss exists either as spores or as dormant protonemata, but in some cases absence is really a measure of lack of collecting inconspicuous non-fruiting upright gametophyte plants. Because of their tiny stature and non-mossy look of their habitats, these taxa are often overlooked by visiting bryologists in a hurry to get as many taxa as possible, so their presence may be much greater than would appear from collection records, and their sporophytic stage is probably over-represented in collections. By targeting such habitats, Kucyniak (1946) found numerous new or rare species in Québec (Jean Faubert, pers. comm.)

Spring and autumn seem to favor ephemerals when more moisture is available than in summer in most habitats, with a number of species visible all winter (Crum 1976 for Michigan, USA): *Ephemerum crassinervium* (Figure 61) late summer to early spring; *Phascum cuspidatum* (Figure 62) November to May; *P. floerkeanum* (Figure 63-Figure 64) October to April; *Acaulon* spores mature in late autumn to spring [*A. triquetrum* (Figure 65), *A. muticum* (Figure 66)]. Michigan spring ephemerals include

Pleuridium subulatum (Figure 67), *Physcomitrium pyriforme* (Figure 68), and *Tortula truncata* (formerly in *Pottia*) (Figure 69); *Ephemerum cohaerens* (Figure 70) appears in both spring and autumn. *Pottia davalliana* (Figure 71) appears in the autumn, but sometimes can be found in summer.

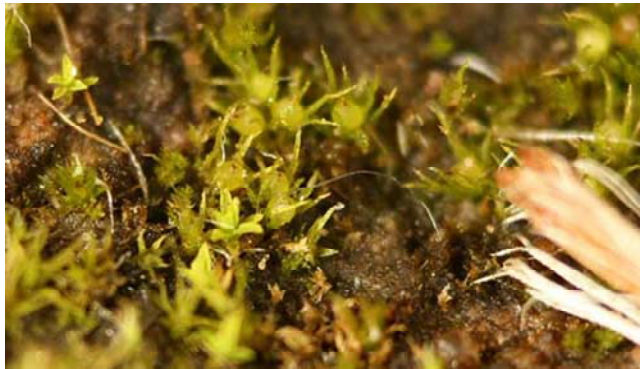


Figure 61. *Ephemerum crassinervium*, an ephemeral moss that grows in the moisture from late summer to early spring. Photo by Bob Klips, with permission.



Figure 62. *Phascum cuspidatum* var. *piliferum*. Photo by David Holyoak, with permission.



Figure 63. *Phascum floerkeanum* (inside red circle), an ephemeral that grows from October to April. Photo by Michael Lüth, with permission.



Figure 64. *Phascum floerkeanum*, an ephemeral that grows from October to April. Photos by Michael Lüth, with permission.



Figure 65. *Acaulon triquetrum* on sand; an ephemeral whose spores mature in late autumn to spring. Photo by Michael Lüth, with permission.



Figure 66. *Acaulon muticum*, an ephemeral whose spores mature in late autumn to spring. Photo by Jan-Peter Frahm, with permission.



Figure 67. *Pleuridium subulatum*, a moss of disturbed agricultural fields and roadsides. Photo by Michael Lüth, with permission.



Figure 68. *Physcomitrium pyriforme*, a spring ephemeral in Michigan, USA, and elsewhere. Photo by Li Zhang, with permission.



Figure 69. *Tortula truncata*, a Michigan, USA, spring ephemeral. Photo by Bob Klips, with permission.



Figure 70. *Ephemerum cohaerens* with perigonia, an ephemeral that appears in spring and again in autumn. Photo by Dick Haaksma, with permission.

It is not surprising that some ephemerals typically produce more than one generation of capsules in the same year. Gray (1935) found that *Aphanorrhegma serratum* (Figure 72) and *Micromitrium tenerum* (as *Nanomitrium austinii*) (Figure 73) have life cycles as short as 62-65 days in Florida, producing two or more sets of capsules per

year. Between these cycles the moss is often buried by floods and silt. Gray surmised that since he always found both mature and immature capsules, these mosses must continuously produce capsules when growing conditions are suitable. Younger plants seem to be produced at the edge of older clumps.



Figure 71. *Pottia davalliana*, an autumn ephemeral that sometimes also appears in summer. Photo by Michael Lüth, with permission.



Figure 72. *Aphanorrhegma serratum*, a species that in Florida has a short life cycle of about two months and that completes that life cycle two or more times a year. Photo by Bob Klips, with permission.



Figure 73. *Micromitrium tenerum*, a species that in Florida has a short life cycle of about two months and that completes that life cycle two or more times a year. Photo by Jan-Peter Frahm, with permission.

It appears that one strategy for these floodplain ephemerals is to produce some sort of survival structure. These may include very large spores, spores that remain in tetrads, and asexual structures that can remain in the mud for a prolonged period of time, then provide a good supply of energy to jumpstart the gametophyte plant when the mud becomes exposed to the sun. Members of the Marchantiopsida, especially members of the genus *Riccia* (Figure 74-Figure 75), seem especially adapted for such strategies (Kürschner & Parolly 1999).



Figure 74. *Riccia sorocarpa* in European floodplain. Photo by Michael Lüth, with permission.



Figure 75. *Riccia beyrichiana* showing folded up lobes that can close up as the plant dries. Photo by Jan-Peter Frahm, with permission.

Wetlands

One might expect that bryophytes growing in wetlands face few problems in dispersing their gametes and might instead time events so that capsules are not submersed or

too humid. But Sundberg (2002) found that even in this "wet" habitat, rainfall of the previous summer had a strong effect on the number of capsules produced, suggesting that gametangia formation was improved under wetter conditions. In wetter peat pits, the amount of precipitation in spring of the same year seemed more important, suggesting that greater precipitation increased sperm dispersal and fertilization. Spore dispersal in *Sphagnum* is indeed facilitated by dry air, but summer droughts can cause premature drying, which negatively affects spore dispersal. At least some *Sphagnum* species grow best at higher temperatures, around 35°C (Li 1991), but it seems that growth might need to compete with spore production. All the species in Sundberg's study release their spores from the beginning of July to the end of August (summer in the North Temperate Zone), with up to a month difference in release times among the species present. Even in this wet habitat, there are dry seasons and wet seasons.

Aquatic

In aquatic habitats, winter may be the best growth period. Glime (1987b), found that in the Keweenaw Peninsula of Michigan, USA, where snow covers the ground about five months of the year, the lake and stream moss *Fontinalis duriaei* (Figure 76) takes advantage of its C₃ metabolism and begins new growth in November, continuing through winter, then accelerating from February to June, with little subsequent growth until cooler weather returns. Laboratory data on temperature effects on growth of six *Fontinalis* species suggest this is a general trend in the genus (Glime 1984, 1987a, b, c).

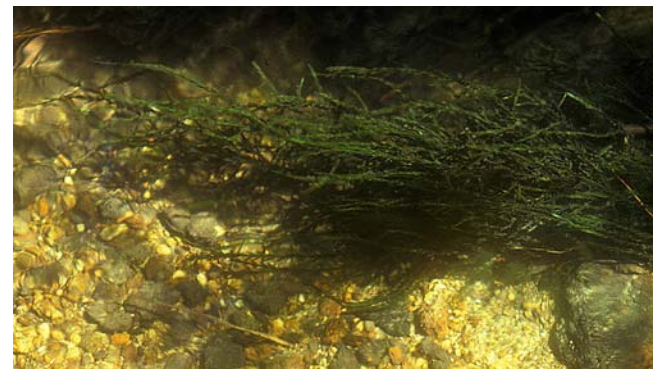


Figure 76. *Fontinalis duriaei* in Japan, a moss that begins its growth season in November. Photo by Janice Glime.

For populations of *Fontinalis*, Glime (1984, 1987a) found that on Isle Royale and in the Keweenaw Peninsula of Michigan, USA, several species produced gametangia in September prior to resumption of growth. In this genus, autumn production of gametangia might be a means to facilitate movement of sperm in small puddles of water and on moist but not submerged mosses, reducing loss of sperm downstream due to strong currents. Once winter begins, these species of *Fontinalis* are completely submersed and this permits the development of the sporophyte in a fully hydrated state. *Fontinalis* species respond to photoperiod, having peak gametangia maturity in autumn and producing capsules in February. Temperatures soon become too warm in summer for aquatic bryophytes that generally remain hydrated, even when stranded above water. The easiest season for many of them to disperse sperm is

autumn as water levels rise and dispersal is facilitated. Temperatures are cool enough for photosynthetic activity and the plant is almost guaranteed of remaining cool and hydrated following fertilization.

But the big surprise came when we found abundant capsules on *Fontinalis dalecarlica* (Glime 1984) and *F. novae-angliae* (Figure 77; Glime 1987c) in February in New Hampshire, USA. These capsules were abraded by spring runoff and had disappeared by the time the snow had melted. No wonder most bryologists think the genus almost never has capsules! No one is looking in midwinter. It appears that archegonia mature in the short days of September and the capsules are most likely the product of that fertilization season.



Figure 77. *Fontinalis novae-angliae* with capsules in February. Photo by Janice Glime

Summary

The life cycle of a moss can be described based on those stages that are observably different, are discontinuous, and require a change in environmental conditions. This definition presents us with the recognizable stages of embryonic calyptra, seta with calyptra, green capsule with calyptra, operculate post-meiotic capsule, de-operculate capsule, spore with bulging wall, protonema, protonema with bud, juvenile stem, antheridium, archegonium.

Growth requires sufficient moisture, nutrients, and light at a time when the temperature does not cause a high level of respiratory loss, below 25°C for most shade-adapted taxa. Growth usually ceases in hot summers when the temperature is too high and carbon loss would be greater than carbon gain, and in cold winters when there is no free water and bryophytes go dormant. Optimal temperatures for elongation, bud formation, and rhizoid production may differ. Furthermore, increase in biomass may occur without increase in height. There is a trade-off between growth and reproduction so that growth diminishes or ceases during reproduction. Chlorophyll concentrations generally increase in response to decreasing light intensity, thus responding to seasonal changes.

Gemmae are more likely than other life cycle events to lack seasonal behavior, but their production may cease during sexual reproduction due to competition for energy.

Antheridia generally initiate before **archegonia** and require longer for development. Many will begin development, then become dormant during winter, resuming in spring to mature when archegonia, initiated in spring, are also mature. Reproduction may be coupled with photoperiod, light intensity, and temperature, and these will most likely be coordinated to provide the reproductive bryophyte with the greatest possibility of sufficient water for fertilization. Nutrients and pH may also play a role in signalling onset of sexual reproduction.

Cross-fertilization in monoicous bryophytes is supported by **protogyny** and **protandry** in many taxa. In dioicous taxa, the perigonia (housing antheridia) are typically initiated first and mature at about the same time as perichaetia (housing archegonia).

Desert bryophytes may have multiple periods of dormancy interrupting any of the developmental stages. Some take advantage of cooler temperatures and greater availability of water in winter to accomplish fertilization. Aquatic bryophytes such as *Fontinalis* may have fertilization in autumn when water levels are rising, ensuring water for development, then produce capsules in winter when spring runoff can aid dispersal.

Sporophyte maturation of most taxa is timed for dispersal during the dry season and may last from only a few days to several years. For most temperate zone bryophytes, spring and autumn seem to be the best time for dispersal. Elevation generally meant that events start later in the year, but higher light levels and in some cases longer days, along with innate adaptations, may cause stages to mature in less time than at lower elevations.

Acknowledgments

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CHAPTER 4-3

ADAPTIVE STRATEGIES: PHENOLOGY, A *SPHAGNUM* CASE STUDY

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CHAPTER 4-3

ADAPTIVE STRATEGIES: PHENOLOGY, A *SPHAGNUM* CASE STUDY



Figure 1. *Sphagnum fimbriatum* with operculate capsules in midsummer. Photo by Janice Glime.

***Sphagnum*: A Case Study**

The easiest way to understand any phenomenon is to examine an example. The detailed phenological study by Pujos (1992) of *Sphagnum fimbriatum* in Haute-Normandie and *S. fuscum* in Québec provides us with this opportunity.

Most of us think of *Sphagnum* as living in wet places, but in fact, its growing tips are often under drought conditions. As the water level falls in the summer, the tops of hummocks are dry, and in winter, the water is frozen, thus creating desiccating conditions. Consequently, the apex of the moss often lacks sufficient water to carry on photosynthesis. This results in considerable variation within the genus regarding the months of photosynthetic activity and growth. Hulme and Blyth (1982) found that species that live in hollows, such as *S. cuspidatum* (Figure 2) and *S. auriculatum* var. *inundatum* (Figure 3), had a longer growing season (10-12 months) than did hummock species such as *S. papillosum* (Figure 4), *S. magellanicum* (Figure 5), and *S. capillifolium* (Figure 6) (5-7 months).

For *Sphagnum fimbriatum* (Figure 7) in Haute-Normandie and *S. fuscum* (Figure 8) in Québec, it appears that despite their ability to grow best at the warm

temperatures of summer, they become sexual in the cooler, probably wetter, conditions of fall (Pujos 1992).



Figure 2. *Sphagnum cuspidatum*, a species of hollows and bog pools. Photo by Michael Lüth, with permission.



Figure 3. *Sphagnum auriculatum*, a species of inundated areas. Photo by Janice Glime.



Figure 4. *Sphagnum papillosum*, a hummock species. Photo by Michael Lüth, with permission.



Figure 5. *Sphagnum magellanicum* forming a hummock. Photo by Michael Lüth, with permission.



Figure 6. *Sphagnum capillifolium capillifolium* on top of a hummock. Photo by Barry Stewart, with permission.



Figure 7. *Sphagnum fimbriatum* habitat. Photo by Dick Haaksma, with permission.



Figure 8. *Sphagnum fuscum*, a hummock species, in its vegetative state. Photo by Michael Lüth, with permission.

Gametangia

In both species studied, antheridial branches (Figure 9) appear first at the end of summer, with the antheridial stalk forming before the antheridium. Although the antheridium develops rapidly, **spermatogenesis** (formation of sperm) spans two months. Like so many other perennial

bryophytes, archegonial development begins somewhat later in Haute-Normandie, in September, requiring about one month for development.



Figure 9. Antheridial branches displaying typical red color. Photo by Janice Glime.

Fertilization

Perichaetial leaves grow much larger than other leaves and protect not only the archegonia, but the developing capsule as well. However, fertilization is delayed until February, at least in Normandie, occurring as the temperature first begins to increase at the end of winter. Archegonial neck cells break down and form mucilage at about the same time the antheridia dehisce. Fertilization of *S. fimbriatum* (Figure 10) in Normandie in 1991 occurred in March.



Figure 10. *Sphagnum fimbriatum*. Photo by Dick Haaksma, with permission.

Embryogenesis (formation of embryo)

By early April, the embryo begins penetrating the branch beneath it and by the end of April mucilage completely surrounds the embryo. It is not until mid-May to June that **sporogenesis** (formation of spores, starting with meiosis) occurs and still another month passes before the pseudopodium (gametophyte extension that becomes a stalk to support the capsule) emerges with the capsule at its apical end (Figure 11).



Figure 11. Mature capsules of *Sphagnum palustre* with capsules still enveloped in perichaetial leaves before the pseudopodium elongates. Photo courtesy of Zen Iwatsuki.

Spore Release and Germination

Spores mature in July and changes in temperature and humidity cause the capsule to shrink, forcing the operculum off (Figure 12). Spores in both species germinate immediately after release (in the lab), producing a thalloid gametophyte and ultimately a single upright plant. But again, we know nothing of what happens in the field. Is there a dormancy, perhaps brought on by temperature or humidity, that delays the spore germination? How long does the protonema persist before the leafy plant develops? How long does it then take the leafy plant to reach sexual maturity?



Figure 12. Capsules after dehiscence and dispersal, with elongated pseudopodium, in *Sphagnum palustre*. Photo courtesy of Zen Iwatsuki.

Summary

In *Sphagnum fimbriatum* in Haute Normandy, as in most mosses, antheridia appear first, in this case late summer, developing over two months. Archegonia begin development in September and require only one month. Fertilization occurs in February or March at the end of winter. The capsule is mature in mid-May to June and sporogenesis occurs, but the pseudopodium requires another month before it elevates the capsule. Spores are released in July and can germinate immediately, but field behavior is unknown.

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CHAPTER 4-4

ADAPTIVE STRATEGIES:
PHENOLOGY TRADEOFFS

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CHAPTER 4-4

ADAPTIVE STRATEGIES: PHENOLOGY TRADEOFFS



Figure 1. *Hylocomium splendens* with sporophytes and young shoot showing new growth of an unexpanded branch to their right. Photo by Janice Glime.

Tradeoffs

Just when you think you have solved all the problems, you discover that the solution has created a new problem. So it is with life, and so it is with optimizing the events in the life of a plant. Large spores give the plant a better start, small ones travel farther. Lots of spores give more chances for landing at a suitable time on a suitable spot, but their survival chances are lower. But what sorts of numbers are we talking about?

Finding this information is not easy, as few papers are written expressly for the purpose of comparing these numbers. We need a concerted effort to put together a representative list. A few are shown in Table 1.

In an organism where the male gamete must disperse without a very specific carrier and the female is stationary, we assume that more males are needed to service the females because many males will be unsuccessful. Rydgren and Økland (2003) stated that we still do not know if bryophytes exhibit reproductive costs (energy costs). Meager evidence suggests they do.

Table 1. Comparison of numbers of reproductive parts of bryophytes. This table is in no way representative.

<i>Octoblepharum albidum</i>	Pôrto & de Oliveira 2002
archegonia	6.7 per perichaetium
antheridia	13.4 per perigonium
<i>Sematophyllum subpinnatum</i>	de Oliveira & Pôrto 2001
archegonia	3-26 per perichaetium
antheridia	8-20 per perigonium
<i>Sphagnum</i>	Sundberg 2002
sporophytes	0.64-20 per dm ²
spores	16,000,000 per m ²
<i>Trichostomum perligulatum</i>	Stark & Castetter 1995
archegonia	2
antheridia	6
<i>Cyathodium bischlerianum</i>	Salazar Allen 2001
archegonia	1-2 per involucre
<i>Plagiochila adianthoides</i>	Johnson 1929
antheridia	22 per spike
sperm	25,000 per antheridium

Rydgren and Økland (2003) compared non-sporophyte-producing and sporophyte-producing sub-population of *Hylocomium splendens* (Figure 1) for five years. They found that indeed the plants with sporophytes had less size development of daughter segments, a lower branching frequency, and fewer new annual segments than those individuals with no sporophytes. This reduced development occurs primarily during the time when the capsule expands and spores are produced, suggesting that there is a significant cost for reproduction – a tradeoff.

However, if all the gametangia are accounted for, rather than individuals, this may not be the case. Stark and coworkers (2001), in examining the desert moss *Syntrichia caninervis* (Figure 2), found that when male and female expressing individuals were controlled for **inflorescence** (reproductive organ group) number, there were no significant differences in biomass between the sexes. Surprisingly, among those that were not expressing sexual traits, there was lower biomass, shorter total stem length, fewer branches, and shorter **ramets** (individual member of clone) than in sex-expressing males and females, and there were fewer ramets than there were sex-expressing female individuals. A threshold size seems to be necessary for sexual expression, accounting at least in part for size differences. In fact, for *Syntrichia caninervis* in this study, all individuals weighing more than 2.0 mg evidenced sexual expression. This biomass requirement supports the concept that more energy is needed for sexual expression, likewise supporting the expectation of a tradeoff between growth and reproduction.

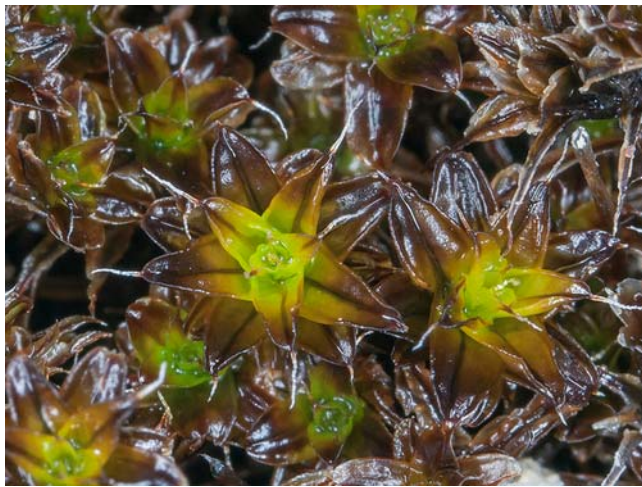


Figure 2. *Syntrichia caninervis*. Photo by John Game, through Flickr Creative Commons.

Tradeoffs with Spore Production

To understand the seasons of sexual reproduction, one needs to understand the tradeoffs within the growth cycle as well. First, there needs to be a sufficient energy supply for either a sexual or an asexual event, and while the formation of sex organs does not seem to produce as much biomass, it is a developmental stage that is costly in energy. Second, the production of gametangia may interfere directly with further growth. In acrocarpous mosses, the gametangia are terminal on the main stem (Figure 3), and once they develop, they inhibit the further development of the stem, at least for that season (Figure 4). Thus,

vegetative growth, in acrocarpous taxa at least, may be strongly limited by time of gametangial production.



Figure 3. *Polytrichum piliferum* splash cups that effectively stop growth of the stem while they are functional. Photo by Janice Glime.



Figure 4. *Polytrichum ohioense* male stems with new growth extended from the splash cups. When the antheridia are developing, further growth of this apex is arrested. Photo by Janice Glime.

Pleurocarpous mosses, on the other hand, develop gametangia on lateral branches and these do not interfere with the growth of the main stems. This difference is further complicated by the fact that most (all?) pleurocarpous mosses are perennial, whereas many of the acrocarpous mosses are annual. Furthermore, one might suppose, the annuals are much more likely to produce capsules (and by implication, gametangia) to permit them to overwinter as spores, whereas many perennials persist by vegetative means only. But, we have very little direct field evidence to support or refute this supposition.

It might be interesting to compare seasons of vegetative growth vs gametangial season in acrocarpous vs pleurocarpous mosses and annuals vs perennials, but data on gametangia are scarce. Among the mosses in Conard's 1947 study, only 15 of the 232 taxa collected had gametangia.

Based on Conard's survey, it appears that peaks in gametangial production in liverworts occur during late spring and again in fall, at least among the 60 Iowa taxa (Figure 5). This is consistent with the report by Zehr (1979) that photoperiod is the dominant factor in gametangial formation in four of the five taxa he studied: *Lophocolea heterophylla* (Figure 6) is day neutral; *Diphyscium foliosum* (Figure 7), *Atrichum angustatum*

(Figure 8), *Trichocolea tomentella* (Figure 9), and *Nowellia curvifolia* (Figure 10) are long-day plants. However, Zehr's sample size is small and Conard's samples may have been biased, since they were subject to seasons favorable for collecting (and collectors), and collectors may be selective in what they collect and keep, favoring plants with capsules over those without.

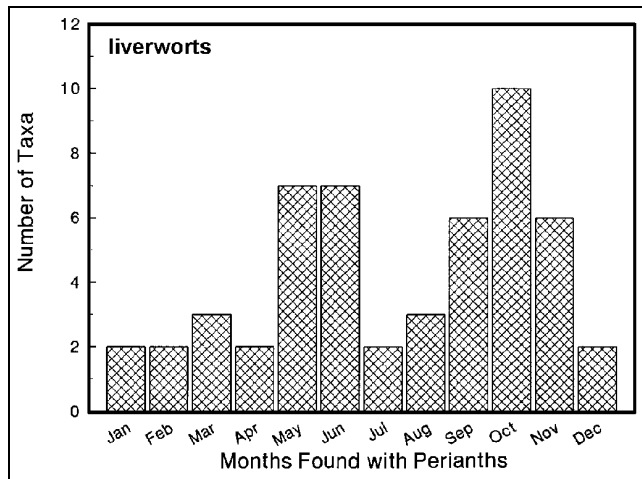


Figure 5. Numbers of taxa with perianths (leafy enclosure of liverwort archegonia) per month among the 30 taxa having perianths out of 60 Iowa liverwort taxa (including Anthocerotopsida) in the herbaria at State University of Iowa and Grinnell College. Based on table from Conard (1947).



Figure 6. *Lophocolea heterophylla*, a day-neutral liverwort, on log. Photo by Janice Glime.



Figure 7. *Diphyscium foliosum* females, a long-day species. Photo by David Holyoak, with permission.



Figure 8. *Atrichum angustatum*, a long-day moss. Photo by Bob Klips, with permission.



Figure 9. *Trichocolea tomentella* from Europe, a long-day liverwort. Photo by Michael Lüth, with permission.



Figure 10. *Nowellia curvifolia*, a long-day liverwort, on a log. Photo by Jan-Peter Frahm, with permission.

It seems that the co-occurrence of fertilization and spore release is relatively common among bryophytes, as seen in the studies of Grimme (1903), Arnell (1905), Lackner (1939), Jendralski (1955), Greene (1960), and van der Wijk (1960). Based on his British experience, Greene (1960) stated that even before a **cohort** (group of individuals with same starting point) of capsules has dehisced, new gametangia are developing. To him, it was "clear" that when sporophytes develop slowly, fertilization may be effected before the previous generation of spores has been released. Likewise, David Wagner (pers. comm.) finds spore and sperm dispersal during the same season in the Northwestern United States. Stark (2001) points out that we have few definitive studies on the duration of spore

dispersal and that in some cases this may last an entire year, as it does with most desert bryophytes.

Two determining factors must be kept in balance to maintain a life cycle: the energy requirements and the growing conditions. For dispersal of sperm, clearly water is needed, and energy must be available leading up to sperm maturation. Spore dispersal is most often favored by dry weather, which as already pointed out, can alternate effectively with wet weather in spring. Spore dispersal itself is a mechanical process and presumably requires no energy. Spore maturation does, but dispersal can wait, being effected in most cases when the capsule dries out, forcing the operculum off. This process likewise might be presumed to require no energy. Therefore, energy requirements may be sufficiently spread over time so that the processes of gametangial maturation and spore/capsule maturation do not compete enough to be detrimental. Once these demands are met, it is beneficial for spores that lack dormancy to be dispersed when good growing conditions are close at hand. The alternating wet and dry conditions of spring would seem to be ideal for this. It remains for us to demonstrate that in fact this is so, since we know virtually nothing about spore germination and protonema development in nature for most species.

Geographic Differences

Both latitude and altitude create different climatic conditions. Inland conditions can be quite different from coastal conditions. The wide range of temperature and moisture created by these geographic conditions imposes strong selection pressures on the genes controlling the phenology of the organisms living there.

Some bryophytes seem to ignore winter, as does *Schistidium apocarpum* var. *confertum* (Figure 11) in the eastern Pyrenees (Lloret Maya 1987). This species, despite living above 1800 meters elevation, is not affected by winter conditions. However, other taxa in these mountains have mature gametangia and fertilization early in the summer with dormant winter sporophyte development followed by rapid maturation of the sporophyte in the first months of summer. At the same time, species living at lower elevations exhibit a continuous progression of stages with no dormancy. Only *Schistidium apocarpum* var. *confertum* behaves this way at high altitudes.



Figure 11. *Schistidium apocarpum* var. *confertum* growing on rock and exhibiting its typical abundant capsules. Photo by Michael Lüth, with permission.

Longton and Greene (1969) demonstrated a latitudinal difference in *Pleurozium schreberi* (Figure 12). In Great

Britain, perigonal development begins in August. Antheridial development apparently is dormant in an immature stage through the winter. Archegonia are first evidenced by perichaetial development in October, but the archegonia likewise overwinter in an immature stage. In spring, both gametangia develop rapidly and fertilization ensues in April and May. The young sporophytes begin to emerge in May, but seta elongation is delayed until August. By October the operculum is in its mature stage, but spores are retained until January, with dispersal occurring January through April – a 9-12 month cycle. Thus, even in this maritime climate, winter is unsuitable for most developmental activities, although presumably winter growth is possible. In France, Finland, and North America, vegetative growth is arrested during the winter, resuming for the period of April to November.



Figure 12. The red-stemmed moss, *Pleurozium schreberi*. Photo by Michael Lüth, with permission.

Measuring winter growth under the snow is difficult. One cannot remove the snow to measure the growth because that would alter the conditions, affecting subsequent measurements. Ideally, one could measure length or biomass just before the first snowfall and just after spring melt, but that is not as easy as it may seem. The first snowfall may only provide temporary cover, followed by a warm period. One cannot be there every day to ensure measurement on the one day that lies just before the permanent winter cover. And spring is not as easy to determine as it might seem. In many habitats, bryophytes are covered with water for a short period of time during and just after snowmelt. Furthermore, the snow may leave, but the air remain cold, or temperatures might rapidly climb to a balmy spring day when there is no more change of state from solid ice to liquid or gas as the snow melts. Predicting and being there and knowing that the patch you measure has just come out from the snow would require being a psychic.

For many bryophytes, those early days following snowmelt are the best time all year for growing as they take advantage of the open canopy and warm but not hot temperatures. But we know next to nothing about the ability of bryophytes to grow under the snow. Could they get enough light through thin layers of snow and enough moisture from partial melt to photosynthesize at times in the winter? Is there a possibility they begin their spring productivity two weeks before they are uncovered? And what about the epiphytes that rest within that funnel of air between the snow and the bark? Are they warm enough

and humid enough to continue photosynthesis throughout most of the winter? Trynoski and Glime (1982) suggest they might, based on finding more bryophytes and bryophyte biomass on the south side of the tree at breast height in Keweenaw County, Michigan, USA.

Longevity Tradeoffs

In 2009, Bryonettters asked "How long do mosses live?" In 2014, Bryonetter Wang Zhe asked about the longevity of bryophytes. There is no satisfactory answer to this question. True, some have very short life cycles, emerging from spores as flood waters recede and completing an annual life cycle within a few months. Others, like *Sphagnum*, may live hundreds of years, dying at the bottom and growing at the top. Others challenge our definition of death, regaining photosynthesis after a long desiccation dormancy.

Thus, the first problem is to determine if the bryophyte is alive. In an organism that thrives on fragmentation, we are confounded by the possibility that a cell or cells remain alive and can under the appropriate conditions begin new growth, often to produce a new plant, a condition known as **totipotency**. In other cases, tissues may remain dormant for years, only to resume growth when getting the light and water they vitally need.

Guy Brassard responded to this query on Bryonet: "This is interesting in a rather odd way. Some years ago, when I was at Memorial University, I found a piece of *Hylocomium splendens* (Figure 1) that I had dried between the pages of a book some 20 years earlier. I put it on a damp paper in a Petri dish on a window ledge without hoping for anything to happen. But, much to my surprise, after about 2 or 3 weeks a NEW BUD appeared on the stem and proceeded to grow into a new branch. So there must have still been some live germ-plasm in the stem of that dried old specimen. If such a tiny piece could remain 'alive' for two decades inside the pages of a book (no water and essentially no light), this means that the time span for air-dried bryophytes retaining live tissue could be much longer (50? 100? years), and that most herbarium specimens are still 'alive' as well!"

This year I watched my moss garden emerge from under the snow after a long and especially cold winter. I was shocked to see that most of the mosses were brown and appeared to be dead. I resisted the temptation to replace them and watched. It took about a month, but green appeared, and most of the clumps now look fully green after a mild, bryophyte-favorable summer. How DO we recognize a dead bryophyte?

The second problem is to determine the age of the bryophyte. As already noted, some mosses have natural annual markers. *Hylocomium splendens* (Figure 1) is named stair-step moss because each year it produces a new primary branch. These stack up like stairs and can be used to determine the age of the moss. *Polytrichum* species have small sections of reduced leaves that mark the end of one year's growth and the beginning of the next (Figure 13). Male *Polytrichum* plants mark each year of growth with the antheridial splash cup (Figure 14-Figure 15). Petraglia (2007) reported *Polytrichastrum sexangulare* (Figure 16) in the Italian Alps as having shoots 9 years in age, with soil humidity apparently influencing longevity (Alessandro Petraglia, Bryonet 25 February 2009). On the

other hand, *Polytrichastrum formosum* (Figure 17) in a Dutch forest has an estimated age of 80-100 years, based on the size of the **genets** (free-living individuals that develop from original zygotes, parthenogenetic gametes, or spores and that produce branches vegetatively during growth) (van der Velde *et al.* 2001). Other genera [*e.g.* *Bryum* *s.l.* (Figure 18), *Schistidium* (Figure 19), *Zygodon* (Figure 20)] have indentations (Rod Seppelt, Bryonet 25 February 2009) similar to those of female *Polytrichum*. But does every plant produce sexual structures every year? How many years pass before the first sexual organs occur on the perennials? Do two rainy seasons cause two growth increments? Do drought interruptions cause growth increments?



Figure 13. *Polytrichum commune* showing growth interruptions (arrow). Photo by Michael Lüth, with permission.



Figure 14. *Polytrichum commune* male innovations, starting a new year of growth from the splash cup. Photo by James K. Lindsey, with permission.



Figure 15. *Polytrichum juniperinum* splash cups with new growth. Photo by Li Zhang, with permission.



Figure 16. *Polytrichastrum sexangulare* from southern Europe. Photo by Michael Lüth, with permission.



Figure 17. *Polytrichastrum formosum*. Photo by David Holyoak, with permission.



Figure 18. *Rosulabryum* (=Bryum) *billardieri* showing three years of growth. Photo by Jan-Peter Frahm, with permission.

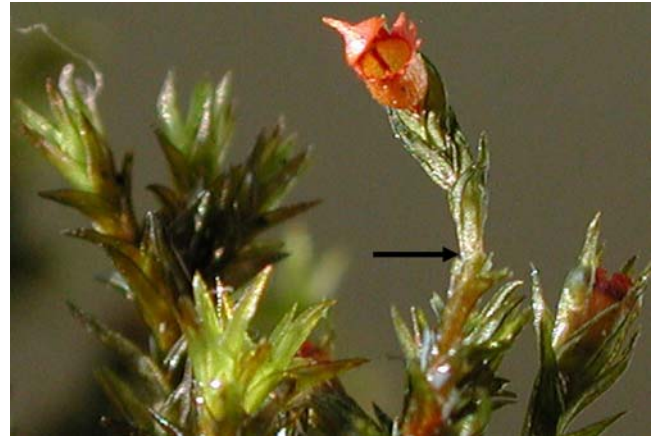


Figure 19. *Schistidium rivularis* showing growth increment (arrow). Photo courtesy of Betsy St. Pierre.



Figure 20. *Zygodon dentatus* showing growth increments (arrows). Photo by Michael Lüth, with permission.

Although this also seemed like a simple question, the answer is often not so simple. As Heinjo During and Martha Nungesser (Bryonet 25 February 2009) pointed out, a single **ramet** (stem/branch) may behave as an **annual** (living only one year), but the **genet** may exist for decades. This seems to be the case for *Crossidium crassinerve* (Figure 21) in the Mojave Desert, USA (Stark & Delgadillo 2003). The problem of genets seems to be further complicated by more extensive sexual reproduction than we often imagine, with males and females arising from one clone and reproducing within a distance of centimeters to several meters, as in *Polytrichastrum formosum* (Figure 17) (van der Velde *et al.* 2001).



Figure 21. *Crossidium crassinerve*, a moss with annual ramets but perennial genets, from Europe. Photo by Michael Lüth, with permission.

As already noted, in *Sphagnum*, some plants may be 100's of years old, but these plants keep dying at the bottom and growing at the top, so one must determine what portion of the plant is still alive before answering any question about its longevity. Yet, Dick Andrus (Bryonet 25 February 2009) found *Sphagnum magellanicum* (Figure 22) measuring 80 cm in Tierra del Fuego and reminded us of Clymo's opinion that *Sphagnum* from a meter or so down could be a 1000 years old. Despite looking old, new plants could be grown from fragments down a meter or more from the surface.



Figure 22. *Sphagnum magellanicum*, a species that Clymo estimated could grow to be 1000 years old. Photo by Michael Lüth, with permission.

In the presumably annual *Crossidium crassinerve* (Figure 21), all is not what it seems to be. Stark and Delgadillo (2003) estimated that some of the stems were as much as 70 years old. Even the older portions were able to produce buds and protonemata in culture.

In the Antarctic, being frozen may suspend biological activity of bryophytes for even thousands of years (Miller 2014; Roads *et al.* 2014; Zimmer 2014). The moss *Chorisodontium aciphyllum* (Figure 23) was removed from a core sample of Antarctic permafrost (Roads *et al.* 2014). Samples from depths of 30, 110, 121, and 138 cm grew, suggesting that they had been preserved in permafrost that was subsequently overrun by a glacier. The stems removed from 110 cm showed evidence of growth *in situ* in ff days. Protonemata arose on rhizoids at the base of the core in 22 days. This older part of the core was estimated to be 1153-1697 years old.



Figure 23. *Chorisodontium aciphyllum* in Antarctica. Photo from Polar Institute, through Creative Commons.

LaFarge *et al.* (2013) found bryophytes emerging from the edge of the Arctic glacier on Ellesmere Island. The radiocarbon dating suggested they had been entombed by the ice during the Little Ice Age (1550-1850) AD. As these often blackened bryophytes emerged, some developed green stem tips or new lateral branches.

Tamás Pócs (Bryonet 18 September 2014) described longevity indicators in cushion-forming bryophytes like *Leucobryum* (Figure 24-Figure 26), *Dicranaceae* (Figure 27-Figure 29), and *Calymperaceae* (Figure 30) when living in seasonal climates. By examining the cushion in section, one can observe yearly layers, much like the annual rings of a tree trunk.



Figure 24. *Leucobryum glaucum* cushions. Photo by James K. Lindsey, with permission.



Figure 25. *Leucobryum* section showing layers. Photo by Lucas. Origin unknown.



Figure 26. *Leucobryum glaucum* clump section showing close view of growth layers. Photo by Walter Obermayer, with permission.



Figure 27. *Campylopus introflexus* (Dicranaceae) cushion. Photo by Michael Lüth, with permission.



Figure 28. *Campylopus introflexus* (Dicranaceae) growth increments exposed by eroding sand. Photo by Robin Stevenson, with permission.



Figure 29. *Campylopus introflexus* (Dicranaceae) indicating growth increments that form layers. Photo by Robin Stevenson, with permission.



Figure 30. *Syrrhopodon involutus* (Calymperaceae) showing layers. Photo by Jan-Peter Frahm, with permission.

How do you determine the age of an individual *Sphagnum* (Figure 31) that can give rise to all populations on the Hawaiian Islands (see Karlin *et al.* 2012)? How do we deal with mosses like *Pleurozium schreberi* (Figure 12) that spread horizontally, dying (?) at the base while continuing growth at the tips? Do we start over in aging them when a branch breaks off, becoming an independent plant?



Figure 31. *Sphagnum fuscum* showing two heads that share a base. Photo by J. C. Schou, with permission.

Richard Zander (Bryonet 18 September 2014) suggested that perhaps it is the diploid (sporophyte) stage that we should measure because it is important in repairing gene damage. He referred to the gametophyte as mostly immortal but genetically degrading.

New methods are making more accurate age determinations possible. Robinson *et al.* (2007) has used ANSTO to make rapid and accurate age determinations from small amounts of material. This technique uses a radiocarbon analysis to determine growth rates based on samples from different portions (5 cm segments) of the plants. They have indicated changes in the growth rates of *Bryoerythrophyllum recurvirostre* (Figure 32) in the Antarctic.



Figure 32. *Bryoerythrophyllum recurvirostrum* from southern Europe, a species with documented changes in growth rate. Photo by Michael Lüth, with permission.

There surely are tradeoffs between longevity and new plants, but such tradeoffs have not really been investigated. We have evidence that spores of at least some bryophytes, for example *Dicranum scoparium* (Figure 33), are unable to germinate when subjected to water extracts of their parents or other members of the same species (Mishler & Newton 1988; Newton & Mishler 1994). Hence, there is a tradeoff between asexual reproduction by ramets and sexual reproduction producing new clones. But which is best for the species? For evolution, sexual reproduction is

usually best because it permits selection against plants with the weaker genomes. But the established genome is obviously adapted to that particular microenvironment.



Figure 33. *Dicranum scoparium* in Michigan, USA, showing what is most likely clonal growth because the adults inhibit the germination of spores. Photo by Janice Glime.

Control of Phenological Events

As implied by the above timing of life cycle stages, phenological events must have internal controls that are called into play by external phenomena. For example, *Funaria hygrometrica* (Figure 34) is under an intricate set of controls that determine where and when it germinates (Hoffman 1966). If it germinates where it is dark, it cannot complete its life cycle.



Figure 34. *Funaria hygrometrica* with developing sporophyte. Photo by Michael Lüth, with permission.

On the other hand, it does germinate over a wide range of both temperature and light intensities (Hoffman 1966). It fails to germinate without light, but can be stimulated to do so by supplying a source of carbon, particularly sugars, suggesting that the importance of light is to provide energy needed to power the process.

Funaria hygrometrica (Figure 34) produces its gametophytes in early spring, produces capsules in the early summer, and sheds its spores in July-September (Hoffman 1966). It fails to germinate on soil treated with nutrients, but succeeds on soil from burned areas. If it

germinates where nutrients are too rich, other plants will be able to grow more easily, so competing plants may shade it before it is able to reach maturity. Humic acids inhibit germination (Raeymaekers, unpub. data.), perhaps accounting for its short life after invasion of a new area.

While it grows well on soil previously heated to temperatures of 200-300°C (sufficient to destroy litter and associated humic acids), *Funaria hygrometrica* (Figure 34) fails to grow on soil previously heated to greater than 300°C. At these high temperatures, N and P are released; addition of these two nutrients to soil previously heated to 600°C permits the moss to grow. Since the moss grows in open areas, it does not benefit from nutrients leached from the canopy, so it is not surprising that addition of K, Ca, and Mg (important canopy leachates) failed to benefit it. The controls at other stages of the life cycle of *Funaria hygrometrica* are less well known, but we do know a considerable amount about the kinds of internal and external controls that are available to mosses, and thus an entire chapter will be devoted to that discussion.

Although we know little about field development of protonemata, we know much about their physiology from laboratory studies, as discussed in the chapter on development. From these, we can surmise the importance of certain environmental controls. Certainly water and light are needed for spore germination. Kinugawa and Nakao (1965) found that photoperiod was important for both germination and protonemal development in *Bryum pseudo-triquetrum* (Figure 35). Both processes required a minimum of 12 hours light, although they could be fooled into thinking they had sufficient light by interrupting a long dark period with only 2 minutes of light.



Figure 35. *Bryum pseudotriquetrum* with antheridia. Photo by David Holyoak, with permission.

Timing of phenological events that bring antheridia and archegonia in the population to maturity at the same time is crucial to reproductive success. Yet different controls seem to guide these two developmental pathways. Hence, as some taxa expand into new geographic areas with different timing of day length, uncoupling of appropriate temperature from appropriate day length, and changes in seasonal moisture regimes, it is not surprising that some fail to produce capsules despite the presence of both sexes. Clearly phenology is an area requiring further

study and may help us understand the success of bryophytes through the widespread areas where we find them. While their morphology has remained relatively unchanged, it appears that their ability to take advantage of seasonal events by a wide variety of phenological strategies, even within a species, may have been evolving rapidly.

Summary

There is a **trade-off** between growth and reproduction so that growth diminishes or ceases during reproduction. Growth also usually ceases in a cold winter when there is no free water and in summer when the temperature is too high and carbon loss would be greater than carbon gain. Optimal temperatures for elongation, bud formation, and rhizoid production may differ. Furthermore, increase in biomass may occur without increase in height. Reproduction may be coupled with photoperiod, light intensity, and temperature, and these will most likely be coordinated to provide the reproductive bryophyte with the greatest possibility of sufficient water. Nutrients and pH may also play a role in signalling onset of sexual reproduction.

Phenological events must not only coordinate with favorable climatic conditions, but they must coordinate with what is occurring among the other occupants of the ecosystem. For example, the non-competitive *Funaria hygrometrica* must grow in early spring, produce capsules in summer, and shed spores starting in July, permitting it to complete its life cycle before the arrival of other plants that compete for light and alter the nutrient regime. Following a fire, it takes advantage of the low nutrients before weathering, microbes, and other plants alter the soil and make it too nutrient-rich. Signals for initiation of life cycle stages often include photoperiod, and the required day length may differ between males and females of a species. Antheridia typically take longer to mature than do archegonia, thus requiring different signals to initiate in order to insure maturity at the same time.

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CHAPTER 4-5

ADAPTIVE STRATEGIES: GROWTH AND LIFE FORMS

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CHAPTER 4-5

ADAPTIVE STRATEGIES: GROWTH AND LIFE FORMS



Figure 1. *Hypnodendron menziesii* demonstrating the clonal growth and dendroid growth form that is possible in a humid climate such as that in New Zealand. Photo by Jan-Peter Frahm, with permission.

Growth Forms and Life Forms

Bates (1998) concluded that life form is a useful concept in bryophyte ecology because of the "exceptionally high dependence of bryophytes on transient external water supplies." He points out that for bryophytes it is not the individual that forms the ecological unit, but rather the clonal or colonial life form (Figure 1). The life form is so constructed as to minimize evaporative loss while maximizing photosynthetic light capture. In the Taymyr Peninsula, Siberia, differences in life form can reduce evaporative rate by 5.3-46 times, depending on the species and site conditions (Vilde 1991).

Definitions

Meusel (1935) describes **growth form** as the overall character of a plant and explains it can only be determined by detailed morphological analysis. It is a purely morphological term, as opposed to **life form**, which is more encompassing and describes the result of life conditions, including growth form, influence of environment, and

assemblage of individuals (Warming 1896; Mägdefrau 1982). **Life form** embodies all the selection pressures that are brought to bear upon a species, or in the words of Mägdefrau (1969), "the organization of a plant in correspondence with its life conditions." Hence, life forms are genetically determined. Growth forms are influenced by the environment.

If these **life forms** persist genetically, we tend to assume they have adaptive significance. Gould and Lewontin (1979) and Mishler (1988) warn us of the trap of this type of thinking. We must recall that selection works against those things that are not beneficial, and that it is a slow process, even slower for those things that convey only a slight disadvantage. Furthermore, such characteristics as life forms may simply carry an occasional advantage, an occasional disadvantage, or little difference from another life form. Correlation of life form with habitat, however, can be used as supporting evidence for the adaptive value of a given life form.

Early classification of **life forms** had little relevance for bryophytes. Dansereau (1957, in Ricklefs 1990) classified plant life forms into trees, shrubs, herbs, epiphytes, lianas (vines), deciduous, evergreen, and bryoids. Raunkiaer (1934) relied primarily on winter characteristics and based his system on bud position:

phanerophytes (*phanero* = visible) – tips of branches; moist, warm environments

chamaephytes (*chamae* = dwarf) – shrubs and herbs, buds near soil; cool, dry climates

hemicryptophytes (*hemis* = half hidden) – die back to ground in winter; cold, moist

cryptophytes (*crypto* = hidden) – buds buried by soil; cold, moist

therophytes (*thero* = summer) – seeds; deserts, grassland

The classification of bryophytes into **acrocarpous** and **pleurocarpous** is somewhat analogous to Raunkiaer's system.

Mägdefrau (1969, 1982) considered that **life form** refers to the habit of the plant in harmony with its life conditions. Hence, life form includes growth form, the assemblage of individuals into formations, societies, or communities, and the influence of external factors. Life form is applied to communities, whereas growth form is applied to individuals. During (1979, 1992) stressed that life forms are linked to the life strategies of bryophytes.

Mishler (Bryonet 1996) takes a somewhat different approach by identifying three terms. He separates **architecture**, considering that to be the most fundamental expression of "internal" factors (genotype and development). This is determined by basic units of growth and their patterns of differentiation. **Growth form** is the middle condition, expressing a mixture of internal and external (environmental) factors and is expressed by the appearance of the stem in the habitat. **Life form** is likewise a mixture, but relies more heavily on external factors. It refers to the overall appearance of the whole colony. Mishler points out the importance of the hierarchical level we are examining – module, stem, or colony.

In response to the confusing array of definitions and uses of the terms life forms and growth forms in the literature, La Farge-England (1996) attempted to give a more precise definition, based on the early usage of the terms. She defined **life form** as "the structures and assemblage of individual shoots, branching pattern, and direction of growth, with modification by its habitat (*i.e.*, cushion, turf, dendroid, mat, pendant, *etc.*).". She emphasizes that the term **life form** applies to the **assemblage**. **Growth form**, by contrast, applies to the structures of the **individual shoot**, including direction of growth, combined with length, frequency, and position of branches. For example, a dense *Grimmia* (Figure 11) cushion is a life form that has responded to its xeric habitat and is a conglomerate of individuals. Its **growth form** would be erect stem, with variable numbers of branches, positioned along its stem (*i.e.* acrotonous or distally versus basitonous or proximally). Like Mishler, she asserts that **growth form** is really architecture of the individual shoot combined with the direction of growth.

Both Mishler and La Farge-England emphasize that the direction of growth does not necessarily imply

perichaetial position. Mishler suggested that *Hedwigia* (Figure 2) is a good example of this uncoupling. It is an acrocarpous moss with a prostrate growth form like that of most pleurocarpous mosses.



Figure 2. *Hedwigia ciliata* showing terminal (acrocarpous) capsules (**top**; photo by Robert Klips, with permission) and horizontal growth form (**bottom**; photo by Janice Glime)..

Jargon of Life History

First, perhaps it is necessary to distinguish between **life history** (or life cycle) traits and **life forms**. As During (1979) points out, **holomorphy** (total form, Hennig 1966; the German *Gestalt*) of plants resulting from their adaptations to their environments certainly relates to their **life strategies**. However, the **life strategy** refers to life cycle characteristics and their timing (treated in the next chapter), whereas **life form** refers to the morphological characters of individuals as well. La Farge-England (1996) points out the inconsistencies in the literature regarding the term **life form** and supports Barkman (1979) by defining it as "the overall organization of growth form, branching pattern, general assemblage of individuals, and modification of a population by the environment." **Growth form**, she reminds us, is "the structural architecture of the individual moss plant." But such architectures can be modified by the environment, hence merging life form and growth form (Tangney 1998). It would seem simpler to define one as the genetically programmed form and one as the environmentally modified form, but the muddle in the literature has crossed those lines with both terms. Thus,

even with the foregoing definitions, confusion in the use of terms will still be with us and I shall make little attempt to unravel their use in the literature presented here. Therefore, interpretation of their use should be done with caution.

Growth Forms

Since **growth form** is the simpler result of genetics, we should examine that first. Meusel (1935) applied the term growth form to individual shoots. It is therefore a purely morphological term expressing the architecture of the plant. As La Farge-England (1996) stated, the terminology of growth form, branching pattern, and position of perichaetia have been used inconsistently in the literature. This morass of literature makes it difficult to compare studies and to sort out the real meanings in nomenclature. After an extensive review of the literature and usage of the terminology, she recommended the following interpretations:

1. **Growth form** is distinct from **life form**.
2. Direction of growth does not necessarily imply perichaetial position; some **acrocarpous** mosses (having terminal perichaetia) grow horizontally, whereas some **pleurocarpous** ones (having perichaetia in lateral buds or on short side branches) grow erect.
3. **Cladocarpus** (Figure 3) is distinct from pleurocarpy, with perichaetia terminal on lateral branches and with juvenile leaf development similar to that on vegetative branches; perichaetial branches have lateral primordia that potentially develop subperichaetial branches. (It is defined in *Glossarium Polyglottum Bryologiae* as a type of pleurocarpy having sporophytes borne terminally on short lateral branches, as in *Fontinalis*).
4. **Pleurocarpy** is defined as having perichaetia terminal on lateral innovations that appear sessile and swollen along supporting axes. Juvenile leaves are morphologically different from those of vegetative branches. Perichaetial innovations lack lateral branch primordia and thus do not produce subperichaetial branches. Pleurocarpy is restricted to **Hypnales**, **Hookeriales**, and **Leucodontales** (Figure 6d), including **Spiridentaceae** and **Racopilaceae**.

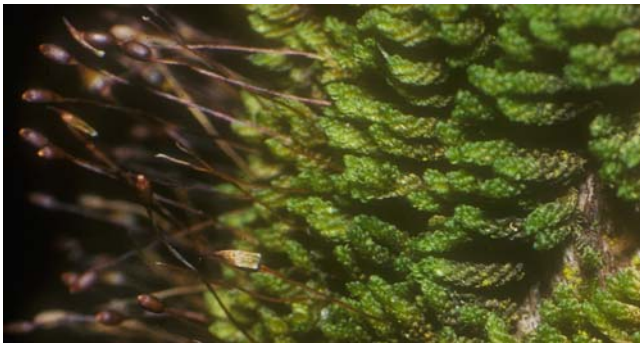


Figure 3. Cladocarpous branches of *Macromitrium microstomum*. Photo by Janice Glime.

But traditionally, growth forms of mosses have been divided into those that are **acrocarpous** (Figure 4) and stand vertically (**orthotropic mosses**) and those that are **pleurocarpous** and lie horizontally relative to the substrate (**plagiotropic mosses**; Figure 6) (Meusel 1935). This of

course leaves a few out of the scheme, as noted by La Farge-England. The orthotropic mosses can be further divided into the **protonema mosses** (Figure 5), with short or non-existent shoots that wither after the sporophyte is produced, and **turf mosses**, with upright shoots that bear new shoots after the sporophyte forms and subsequently bear further archegonia and more sporophytes; these new growths are the **innovations**. The **plagiotropic mosses** (Figure 6) include **thread mosses** (e.g. *Leskeaceae*, some *Amblystegiaceae*), with little difference between the main stem and lateral branches, **comb mosses** (e.g. *Hypnaceae*, *Brachytheciaceae*, *Meteoriaceae*), with a strong main shoot with many simple or branched lateral branches, and the **creeping-shoot mosses** (e.g. *Leucodon*, *Antitrichia*, *Climaciaceae*, *Hypnodendraceae*), with rhizomatous main shoots that give rise to upright main shoots.



Figure 4. Acrocarpous growth form exhibited by *Oncophorus wahlenbergii*. Photo by Michael Lüth, with permission.



Figure 5. Protonema mosses. **Upper:** *Pogonatum aloides*. **Lower:** *Buxbaumia aphylla*. Photos by Michael Lüth, with permission.

The same species may exhibit more than one growth form. For example, in some populations *Hylocomium splendens* (Figure 7) exhibits **monopodial growth** (single central axis with apical growth) (Ross *et al.* 1998, 2001). However, some populations can continue by **sympodial growth** (growth produced by lateral buds just behind apex).



Figure 6. Plagiotropic, pleurocarpous, perennial mosses. **a & b.** creeping shoot mosses – *Antitrichia curtipendula*. **c.** creeping shoot moss – *Climacium dendroides*. **d.** creeping shoot moss – *Leucodon brachypus* var. *andrewsianus*. **e.** thread moss – *Amblystegium serpens*. **f.** thread moss – *Leskea polycarpa*. **g.** comb moss – *Brachythecium reflexum*. **h.** comb moss – *Hypnum sauteri*. **a, b, e-g** photos by Michael Lüth, with permission; **c, d** photos by Janice Glime.

In forest habitats of temperate to mid-arctic regions the growth of *Hylocomium splendens* (Figure 7) is primarily sympodial, creating the stair-step form that easily delineates annual growth (Ross *et al.* 2001). Higher nutrient availability promoted sympodial growth. In tundra and high arctic habitats, monopodial growth predominates and increments cannot easily be discerned. Transplant experiments demonstrated that these traits were plastic, but that natural variability was greater among those shoots in natural populations at transplant sites, indicating a genetic component as well as an environmental component to the differences, affecting both growth and life forms.



Figure 7. Weft life form of *Hylocomium splendens*, exhibiting well-defined annual branching. Photo by Michael Lüth, with permission.

Ross *et al.* (1998) found that the sympodial *Hylocomium splendens* (Figure 7) plants had increasing stiffness with stem segment age and flexibility decreased with age up through four years, then declined. However, monopodial plants showed neither of these age effects and no increase in stem diameter with age. The sympodial stems had significantly more cellulose than their monopodial counterparts, providing them with a higher stress yield. The predominance of these two forms differs with habitat, with more northern populations lacking the sympodial branching that defines the annual increments. Økland (2000) further determined that reproductive capacity differs with stem position and age. The apical tips are subject to greater exposure and are less likely to have successful reproduction. Reproductive failure is greatest for older segments buried within the weft (44%), lowest for intermediate vertical positions (12%), and relatively high for the emergent segments. The greatest annual increment is likewise at this intermediate level (2-10 mm below the bryophyte surface) where there is still sufficient light but the loss of water is minimized.

Økland (2000) pointed out the importance of "growth form" in the way that pleurocarpous and acrocarpous bryophytes interact in competition. In our study on Isle Royale (Raeymaekers, Zhang, & Glime unpubl), the interaction between the acrocarpous *Dicranum polysetum* (Figure 8) and the pleurocarpous *Pleurozium schreberi* (Figure 8) differed from year to year, most likely depending on the precipitation patterns. In some years, *D. polysetum* increased in area and overran *P. schreberi*, but in other years the reverse occurred. Økland suggested that the relationship of upper segments to lower ones represented **amensalism**, where the lower segments were

harmful. Small segments were more easily buried. This relationship can play an important role in both intraspecific and interspecific interactions among bryophytes.



Figure 8. *Pleurozium schreberi* (diagonally at lower right) competing with *Dicranum polysetum* (upper left). Photo courtesy of Herschel Horton.

Life Forms

Literature on life forms and growth forms is confusing because different authors have used the terms in different ways, sometimes in reverse of the descriptions above. Even in the long-studied tracheophytes, the terms have often been used as if they are interchangeable. In studying loblolly pine trees, Haney *et al.* (1993) illustrated effects of density on "growth form" of loblolly pine tree shape (Figure 9). They found that in low densities, trees were shorter and had more branches. At medium density, they were taller, but branches were few in number. At high densities, trees were tallest and branches were still few. These environmental influences on tree form fit the more encompassing definition of life form described above by La Farge-England (1996). As expected, allocation of biomass changes relative to density (Table 1), resulting in a different form. Such mosses as *Sphagnum* and *Climacium* (Figure 13c) would be interesting tests of a similar form change in bryophytes. *Climacium* is known to change form, but it appears to be under both environmental and genetic control; effect of crowding was not studied (Shaw 1987).

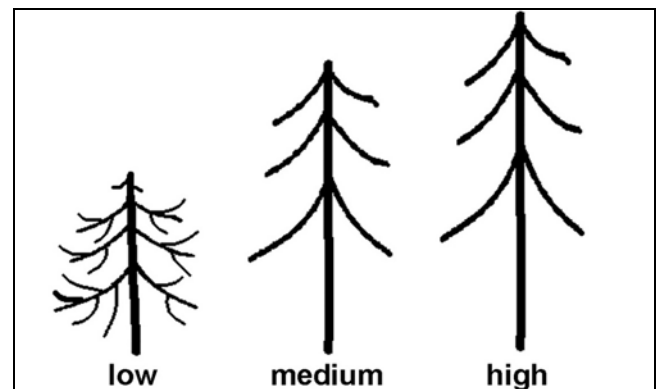


Figure 9. Illustration of forms in loblolly pine at different densities. Based on Haney *et al.* (1993).

Table 1. Allocation of biomass in trees of loblolly pine at three density levels (Haney *et al.* 1993).

	low	medium	high
diameter (cm)	11.87	7.79	6.67
number of whorls	18	11	9
biomass (kg)	12	6.5	4.9
crown ratio	0.79	0.52	0.44
branches	50	27	21
branch length (m)	1.5	1.05	0.9

Bates (1998) raised the question "Is 'life-form' a useful concept in bryophyte ecology?" When he pointed out that most bryophytes are either clonal or colonial, he emphasized that it is these, not individual shoots, that are the functional units. The life form maximizes productivity and minimizes water loss, but it may also function to prevent photoinhibition or scavenge cloud water. Despite its usefulness in indicating moisture and light conditions, Bates considers life form to have limited use "as a framework in ecological studies." He also considers a major problem to be the inconsistent way the concept has been applied in the literature. Life forms also change, as pointed out by Warming (1896). Bates suggested that one interpretation of life form is to consider highly productive horizontal growth forms like that of *Brachythecium rutabulum* (Figure 10) to be an adaptation for **foraging** (horizontal growth that permits mosses to take wider advantage of nutrients and light; Bates 1998). Life forms do not evolve independently and are closely tied to the life cycle and reproductive traits. Nevertheless, Bates concluded that the concept was useful because of "the high dependence of bryophytes on external transient water supplies." However, the description of life form alone will provide insufficient understanding and will depend on knowledge of its relationship to other attributes of the life strategy.



Figure 10. Horizontal growth form of *Brachythecium rutabulum* that may be used for light-scavenging (foraging). Photo by Michael Lüth, with permission.

Age changes the life form and its effect on the physiology of *Grimmia pulvinata* (Figure 11) in a different way (Zotz *et al.* 2000). As discussed in the structural adaptations related to water, this moss forms cushions. As the cushion volume increases, so does the water volume. However, the surface area increases two-dimensionally as the volume increases three-dimensionally, causing a decrease in the surface area to volume ratio. This greatly enhances the water retention of the cushion as it enlarges. On the other hand, the CO₂ exchange decreased with size, again because of the reduced surface area. Lowered CO₂

exchange corresponded with lower rates of both net photosynthesis and dark respiration.



Figure 11. Cushion life form of *Grimmia pulvinata*. Photo by Des Callaghan, with permission.

Nevertheless, life forms are often indistinct from growth forms. A plant is predisposed to a certain growth form, and despite neighbors or environmental conditions, it retains that growth form as part of its life form. In this sense, Mägdefrau (1982) lists ten life forms for bryophytes (Figure 12, Figure 13), to which I (Glime 1968) have added **streamer**.

Mägdefrau Life Forms

- Annuals** – pioneers; no vegetative shoots remain to carry on a second year; *Buxbaumia* (Figure 5), *Diphyscium*, *Ephemerum* (Figure 13a), *Phascum*, *Riccia*
- Short turfs** – open mineral soils and rocks; regenerative shoots; form spreading turfs for only a few years; *Barbula* (Figure 13b), *Ceratodon*, *Didymodon*, *Marsupella*
- Tall Turfs** – forest floors in temperate zones; can conduct water internally; very tall; persist by regenerative shoots; *Bartramiaceae*, *Dicranaceae*, *Polytrichaceae* (Figure 13c), *Drepanocladus*, *Herbertus*, *Sphagnum*, *Tomenthypnum*
- Cushions** – rocks, bark, Arctic, Antarctic, alpine; usually high light; grow upward and sideways; hemispherical; persistent for many years; *Andreaea*, *Grimmia*, *Leucobryum* (Figure 14), *Orthotrichum*, *Plagiopus*, no liverworts
- Mats** – rocks, bark, [on leaves (epiphyllous) in tropics]; plagiotropic and persistent for a number of years; *Lejeuneaceae*, most *Marchantiaceae*, *Homalothecium*, *Lophocolea*, *Plagiothecium* (Figure 13d), *Radula*
- Wefts** – forest floor of temperate zone; hold considerable capillary water; grow loosely and easy to remove from substrate; new layer grows each year; *Brachytheciaceae*, *Hylocomiaceae* (Figure 7), *Bazzania*, *Ptilidium*, *Thuidium*, *Trichocolea*
- Pendants** – epiphytes, especially in tropical cloud forests; long main stem with short side branches; *Meteoriaceae* (Figure 13e), *Phyllogoniaceae*, some tropical *Frullania*
- Tails** – on trees and rocks, shade-loving; radially leafed, creeping, shoots stand away from substrate; *Cyathophorum*, *Leucodon* (Figure 6d), *Spiridens*, some tropical *Plagiochila*
- Fans** – on vertical substrate, usually where there is lots of rain; creeping, with branches in one plane and leaves usually flat; *Neckeraceae* (Figure 13f), *Pterobryaceae*, *Thamnobryum*, some *Plagiochila*
- Dendroids** – on ground, usually moist; main stem with tuft of branches at top; *Climacium*, *Hypnodendron*, *Hypopterygium*, *Leucolepis*, *Pleuroziopsis* (Figure 13g), *Symphogyna hymenophyllum*
- Streamer** – long, floating stems in streams and lakes; *Fontinalis* (Figure 13h)

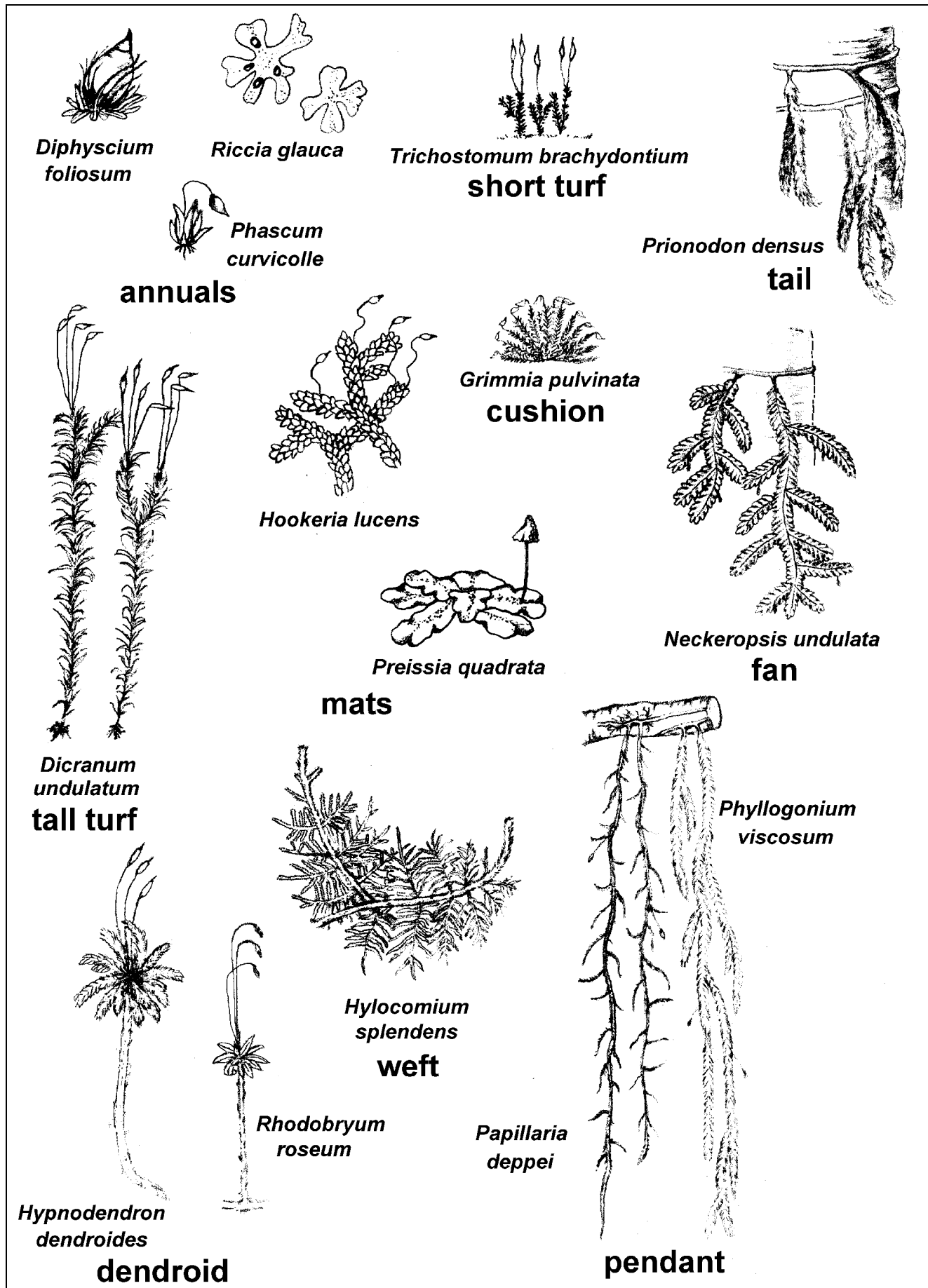


Figure 12. Life forms of mosses and liverworts, based on Mägdefrau (1969). Redrawn by Margaret Minahan.



Figure 13. Life forms of bryophytes. **a.** Annual – *Ephemerum minutissimum*. **b.** Short turf – *Barbula unguiculata*. **c.** Tall turf – *Polytrichum formosum*. **d.** Mat – *Plagiothecium curvifolium*. **e.** Pendant – *Meteorium*. **f.** Fan – *Neckera urnigera*. **g.** Dendroid – *Pleuroziopsis ruthenica*. **h.** Streamer – *Fontinalis antipyretica*. Photos by Michael Lüth, with permission; e & g by Janice Glime.

Environmental Influences on Life Form

These eleven forms may be further divided, as suggested by Horikawa and Ando (1952). As Mägdefrau (1982) points out, light and water are the predominant influences on life forms. Crowded shoots with dense foliage facilitate water movement and retention in areas with sufficient soil water, thus favoring **tall turfs**. **Mats**, **wefts**, **tails**, and **fans**, on the other hand, are unable to obtain water by capillary action, but depend on the capillary spaces to retain water and extend their periods of activity. **Pendants** (Figure 13e) are like laundry on the clothesline and are particularly susceptible to drying; hence they live in places with considerable rainfall or fog, assumedly directing the water to the growing tip. Mägdefrau (1982) cites his observations on mosses near waterfalls to support this assumption.

The **cushion** life form (Figure 14) is highly adapted for water conservation. Proctor (1980) found that the laminar flow patterns over moss cushions were consistent with the measured loss of water from surfaces of varying degrees of roughness. Water loss increased rapidly beyond a critical wind speed, at which the surface irregularities of the cushion could be related to boundary-layer thickness. The thickness of this boundary layer determines the rate of water loss, with thick layers reducing evaporation. Even cushions have turbulent flow as opposed to laminar flow (Rice *et al.* 2001), and the more deeply the air penetrates into the moss canopy, the more turbulent that flow and the greater the evaporation. Among the growth forms, we would expect cushions to have the least turbulence, with wefts and turfs creating more (Figure 15). Surface roughness increases conductance (Rice *et al.* 2001). However, Proctor (1980) found that hair-points of the leaves that project above the cushion surface reduce boundary layer conductance, for example, by about 20-35% in *Syntrichia intermedia* (Figure 16) and *Grimmia pulvinata* (Figure 11), hence serving as an adaptation to reduce water loss.



Figure 14. Cushions of *Leucobryum glaucum* in a mixed hardwood forest in the Keweenaw Peninsula of Michigan, USA. Photo by Janice Glime.

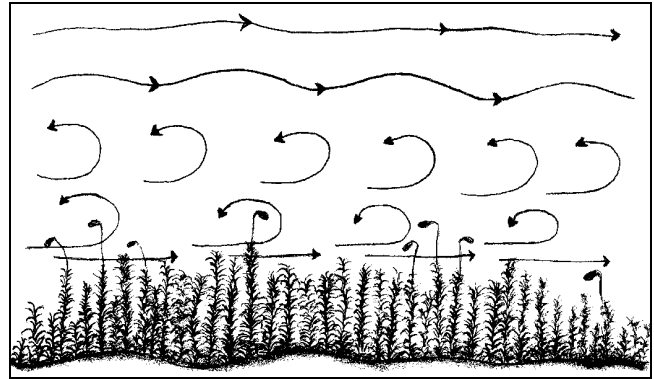


Figure 15. Diagram indicating turbulence and boundary layer as might be found above the irregular surface of a moss weft. Having all stems at the same height, as in a cushion, would reduce the turbulence. Drawing by Margaret Minahan.



Figure 16. *Syntrichia intermedia*, a species with hair points that reduce boundary layer conductance. Photo by Michael Lüth, with permission.

Rice *et al.* (2001) have used wind tunnel experiments to examine effects of architectural features on boundary layer thickness and subsequent water balance of bryophytes. Using evaporation rates of ethanol, they were able to assess differences among 11 taxa having a variety of canopy structures. They accounted for 91% of mass transfer of water loss using models based on surface structure. Even the seemingly smooth surface of cushions behaved as turbulent flow rather than laminar flow boundary layers. Conductance increased with surface roughness, causing those species with greater roughness to have higher conductance rates at all wind speeds.

Water-holding capacity is often more important than obtaining water. In the Antarctic, dense rhizoids contribute to high water-holding capacity in *Bryum algens* (Lewis Smith 1988). In *Schistidium antarcticum* (Figure 17), the **turf** form has a high water-holding capacity, whereas the densely packed **cushion** form has a lower water content relative to its dry weight. Nevertheless, the rate of water loss is much more rapid in the turf form (Lewis Smith 1988). I am puzzled, however, by the more rapid water loss in the more tomentose form of *Bryum algens* than in the form with fewer rhizoids. I would have to conclude that water was held loosely among the rhizoids, contributing to the magnitude of weight loss, and was lost more easily, giving a higher percentage loss. A similar phenomenon could explain the differences between the water loss of the turf and cushion. Lewis Smith found that the reverse relationship holds if the water loss is expressed

relative to the initial water content instead of the dry weight, supporting my interpretation.



Figure 17. Cushions of *Schistidium antarcticum* on Macquarie Island in the Antarctic. Photo courtesy of Rod Seppelt.

Physical factors of the environment also contribute to life form in other ways. Once the growing apex reaches the surface of the **cushion** or exceeds the protection of a rock, it would be exposed to air movement where it would dry out. However, the ethylene concentration around the growing tip would also diminish. Whenever the moss slowed its growth and fell below its fellow cushion members, the higher ethylene concentration trapped within the cushion could again accelerate its cell elongation. Results with *Fontinalis antipyretica* (Figure 13h) suggest that ethylene in mosses reduces cell division but permits and perhaps enhances cell elongation (Figure 18) (Glime & Rohwer 1983). If it indeed acts this way, such a mechanism could be a sensitive and effective control mechanism that would maintain the cushion growth form necessary for maximum moisture retention (Kellomaki *et al.* 1978) and surface light. If, however, ethylene retards elongation as it does in most tracheophytes (Abeles 1973), IAA (indole acetic acid, a growth hormone) is probably the controlling factor. IAA is destroyed by light (Goodwin & Mercer 1983), so those branches getting more light would grow less, not to mention being retarded by desiccation, whereas those within the mat would be shaded and grow more, as an etiolation response. Mosses kept humid in a plastic bag in a place where little light reaches them produce narrow, etiolated shoots. In a terrarium, *Dicranum scoparium* (Figure 19), *Pleurozium schreberi* (Figure 8), and *Brachythecium* (Figure 10) all produce etiolated tips, presumably in response to low light (pers. obs.).

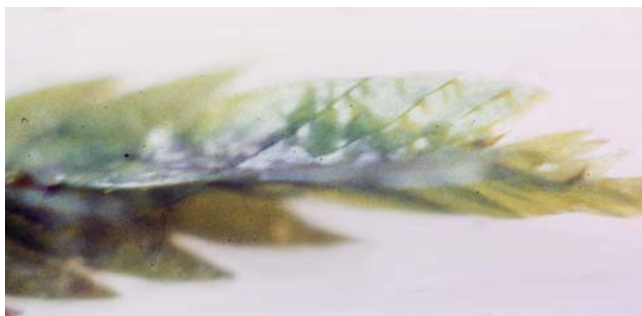


Figure 18. *Fontinalis antipyretica* leaves showing uneven growth effects of ethylene produced by application of ACC. Photo by Janice Glime.



Figure 19. *Dicranum scoparium*, a species that becomes etiolated in very low light. Photo by Janice Glime.

Plants, including bryophytes, have specific mechanisms to combat light intensity changes. Species from open habitats respond to simulated shade with a large increase in stem elongation (Morgan & Smith 1981). This increase would carry the plant upward until it topped its competitors and could receive the needed sunlight. Lignified woodland species react much less or not at all; here the futile attempt to top the canopy would result in tremendous amounts of wasted energy. **Cushion** bryophytes, however, respond to shading by each other like species from open habitats. In nature we see rounded cushions of *Leucobryum* (Figure 14) and *Dicranum* (Figure 19), and we must wonder if the tall center plants and short border plants are merely a function of age. Yet when a clump is backed up against a rock, it is not as short on the rock side as it is on the other side, but rather it tapers down and away from the rock. Is it light intensity acting on IAA, exposure to desiccation, or ethylene concentration that maintains these cushions, or some combination of these?

In mangrove swamps, Yamaguchi and coworkers (1990) found that small, **appressed** liverworts, especially **Lejeuneaceae** and **Frullaniaceae** (Figure 20), predominated, whereas in more landward sites the larger **ascending** taxa such as *Plagiochila* (Figure 21) and pleurocarpous mosses were found. This distribution seems counter-intuitive unless the seaward sites were more subject to wind desiccation from buildup across the water, whereas the more landward ones were protected by the forest. Salt tolerance may enter the relationship as well, but this has not been explored.



Figure 20. *Frullania tamarisci* illustrating the compact growth form of the genus. Photo by Hermann Schachner, through Creative Commons.



Figure 21. *Plagiochila* sp. illustrating the loose growth form of this liverwort. Photo by Lin Kyan, with permission.

Birse (1957) showed that a normally monopodial dendroid *Climacium dendroides* (Figure 13c) can be induced to grow horizontally as a stolon when affixed to a substrate and supplied with ample moisture. It furthermore will reverse its direction of growth if turned upside down, yet, if placed in a moist pot, it will follow the substrate, growing down on the outside of the pot and ignoring gravity. If buried in sand, it will regenerate shoots that Birse *et al.* (1957) observed to grow up to the surface, then grow horizontally. She likewise observed that *Thamnobryum alopecurum* (Figure 22-Figure 23) exhibited growth forms ranging from simple branches in dripping water (Figure 22) to highly dendroid in very moist air (Figure 23).



Figure 22. Simple branching of *Thamnobryum alopecurum* in dripping water. Photo by David Holyoak, with permission.

Aquatic mosses such as *Fontinalis* (Figure 13h) do not fall easily into the above classification system. While most *Fontinalis* species hang in a pendant form similar to pendant epiphytes, their physiological relationship to their environment as a result of this growth form is quite different. The tip, instead of receiving water dripping down from the remainder of the plant, is immersed most of the year. This long form, which I have termed **streamer** (Glime 1968; Jenkins & Proctor 1985) is more likely a

result than an adaptation. The persistent growth of this moss permits it to grow farther and farther from its substrate, but many branches stack upon each other to make a thick weft, but one that is not easy to remove from the substrate. In *Fontinalis dalecarlica* (Figure 24), rhizoids are generally restricted to bases of stems, and the long, persistent stems are extremely strong (Glime 1980). In *F. novae-angliae* (Figure 25), rhizoids can originate throughout the stems, especially on the stolons, making a firmer attachment to the substrate. It would be interesting to examine competition in these two taxa since they can occupy the same streams and even the same rocks.



Figure 23. Dendroid form of *Thamnobryum alopecurum* in moist air. Photo by Des Callaghan, with permission.



Figure 24. *Fontinalis dalecarlica*, a species that produces rhizoids only at its base. Photo by Jan-Peter Frahm, with permission.



Figure 25. *Fontinalis novae-angliae*, a species that forms rhizoids along its stems. Photo by Janice Glime.

Although many studies describe dominant life forms, these descriptions are rarely based on quantitative data. Kürschner (1994) used mean cover values to describe life

forms on basic rocks in nine communities in southern Germany on the northern border of the Schwabische Alb. He found that communities subject to high light and temperature (photophytic and thermophytic) were dominated by cushions, short turfs, and perennial and short-lived colonists (life strategies discussed in the next chapter). As these graded into shady habitats, wefts and mats were more common, with perennial shuttle and perennial stayer life cycle strategies; reproduction was more "passive." Low light species (sciophytes) and aquatic species were perennial fan-formers with sexual reproduction.

Whereas growth form is important for water and light relations, we seldom speak of in relative to support. Nevertheless, with no lignin, bryophytes cannot grow very tall due to lack of support, utilizing cushion growth forms to provide support in some species, especially in *Polytrichum* and its close relatives. During *et al.* (2015) examined the relationship of support along an altitudinal gradient in northern Japan, using *Pleurozium schreberi* (Figure 8) and *Pogonatum japonicum* (Figure 26) as model organisms. *Pogonatum japonicum* had thicker stems, greater rigidity, and exhibited more effect with altitude than did *P. schreberi*. Both exhibited thinner stems and greater stem flexibility with increasing altitude. To me this was a surprising result, based on the knowledge that in tracheophytes wind causes stems to thicken due to greater production of ethylene (Biro *et al.* 1980). I would expect greater winds at higher altitudes. This is an interesting observation that needs to be replicated in other species on other altitudinal gradients.



Figure 26. *Pogonatum japonicum*, a species that exhibits thinner stems and greater stem flexibility with increasing altitude. Photo from Digital Museum, Hiroshima University, with permission.

Some stems can develop considerable stem stiffness and strength, as indicated by biomechanical tests (Frenzke *et al.* 2011). This is achieved by a dense hypodermal sterome "comparable with that of woody stems." With this strength, such mosses as *Dendroligotrichum dendroides* (Figure 27) are able to stand upright. Differences in stem strength are seen among the species of *Fontinalis*, with *F. dalecarlica* (Figure 24) exhibiting considerable stiffness and strength that permit it to live where there is rapid flow. *Fontinalis flaccida* (Figure 28), on the other hand, has a flaccid stem that cannot withstand the strong flow, forcing it to live in lakes and pools of streams. These differences can be observed as differences in the stems (Figure 29-Figure 30).



Figure 27. *Dendroligotrichum dendroides*, a moss with a strong stem permitting it to stand upright. Photo by Felipe Osorio Zúñiga, with permission.



Figure 28. *Fontinalis flaccida* with perigonia, showing the thin stem for this species that is supported by water. Photo by Janice Glime.

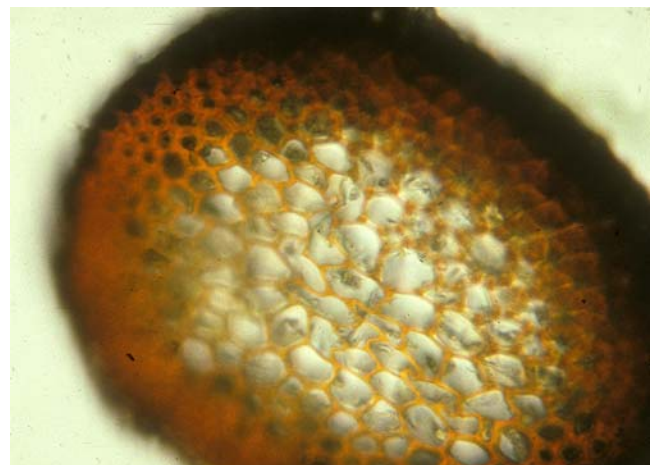


Figure 29. *Fontinalis dalecarlica* cs showing thick-walled cells in outer part of stem. Photo by Janice Glime.

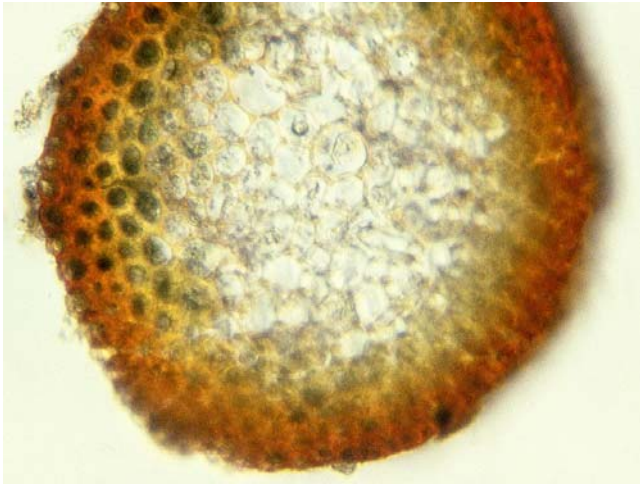


Figure 30. *Fontinalis flaccida* stem cs showing narrower stem and thinner cell walls, especially in the center of the stem. Photo by Janice Glime.

Physical Effects on Growth Form

Moss Balls

The strange phenomenon of moss balls was reported in 1912 by Dixon, who referred to them as "mosses growing unattached." Bryologists still remain fascinated by these strange organisms that grow in a ball and are mobile, so that at different times any part of the sphere may be exposed to sunlight or substrate. But bryologists are not the only ones fascinated by them. In Japan, a monument is dedicated to their preservation (Iwatsuki 1977).

In 1874, the United States sent an expedition to the Kerguelen Islands in the South Indian Ocean to observe the transit of Venus (Mägdefrau 1987). The surgeon of the expedition was also an amateur botanist and an avid collector. He brought back a "curious moss" that seemed "not to be rooted to another plant, but to be blown about by the wind indiscriminately," as described by the bryologist Th. P. James. Schimper later described these same mosses as having a size that varies between that of a cherry and a middle-sized potato. The smaller balls were *Blindia aschistodontoides*, and the larger ones were formed by stems of *Andreaea parallela* by radiating from a central core of soil or a small pebble. Since then similar wind-formed balls have been found in Alaska, Iceland, Norway, on Mount Ontaka in Japan, and even at the high elevation tropics of Mount Kenya, Mt. Elgon, and Mt. Kilimanjaro in Africa.

Such balls in Arctic and alpine areas could result from **solifluction**. **Solifluction** is a slow creeping of fragmented material down a slope over impermeable material, due to the viscous flow of water-saturated soil and other surficial materials, particularly in regions underlain by frozen ground (not necessarily permafrost) acting as a barrier to downward water percolation. Its drift typically occurs at a rate of 1-10 cm per year (White 2001) in relatively cold regions when the brief warmth of summer thaws only the upper meter or two of loose earth materials above solid rock, which becomes waterlogged because the underlying ground remains frozen and therefore the water cannot drain down into it. Mosses could travel and tumble with it (Figure 31).

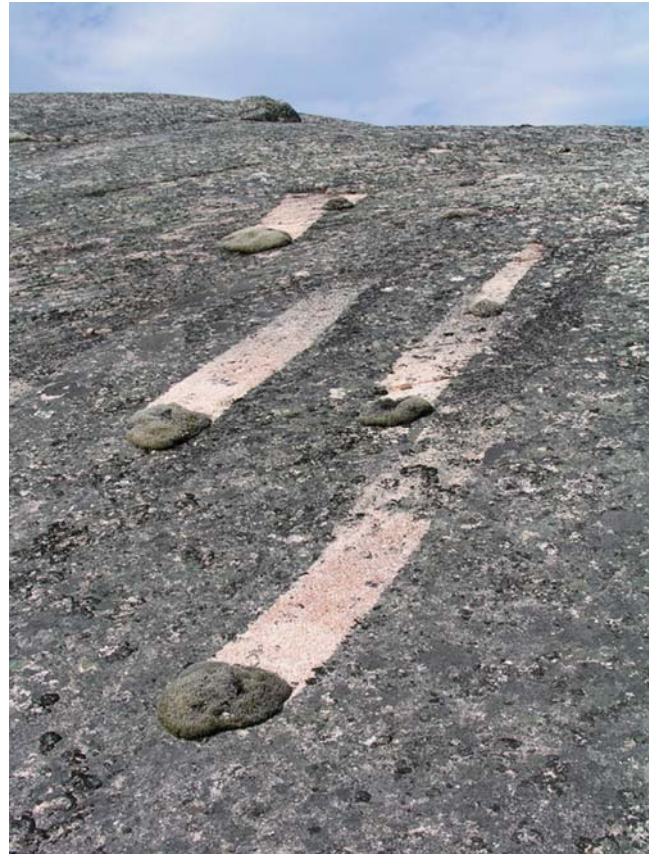


Figure 31. This moss, probably *Grimmia ovalis*, has been termed a galloping moss due to its movement down its substrate. This behavior may be an example of solifluction. Photo by Wouter Bleeker, with permission.

Hedberg (1964) interpreted the African balls (*Grimmia ovalis*, Figure 31; Mägdefrau 1987) to form as a result of solifluction. Mägdefrau (1987) tested this hypothesis by experimenting with balls in Teleki Valley of Mount Kenya at 4200 m. The balls were marked and their locations sketched. When it was dry, there was no solifluction and the moss balls remained in place. However, when they experienced daily watering and frost at night, the balls rotated but held their positions. Rather, it appears that when ice crystals and ice needles form at night, they cause the mosses to be forced away from their substrate and broken off. These freed mosses are blown about continuously and thus grow in all directions, forming balls.

Mägdefrau (1987) observed that none of the mosses in balls had sporophytes, whereas those of the same species growing attached had plentiful sporophytes. He concluded that the growth of sporophytes is prevented by the rolling movement. It would seem likely that young setae and perhaps even archegonia at apices may be damaged by abrasion as they get beaten around over the rocky surface. When mosses lie for a longer period of time on one side, sporophytes develop on the edge of the disk.

On frozen Icelandic soil (Mägdefrau 1982) and Alaskan glaciers (Shacklette 1966; Heusser 1972; Iwatsuki 1976), dislodged mosses blow about across the surface, forming similar balls. During (1992) observes that this life form, which also includes lichen species, results in areas that have high winds and little vegetation.

Perez (1991) attributes the transport of *Grimmia longirostris* moss balls (Figure 32) in the Paramo de

Piedras Blancas of the Venezuelan Andes to needle ice activity. These balls had a high organic content (19%) and a collection of fine mineral grains (69%), a much higher fine grain than in the underlying mineral soils. This combination of organic content and fine grains affords the moss balls a much higher water retention capability than paramo soil, with water-holding capacity increasing with the size of the ball.



Figure 32. *Grimmia longirostris* solifluction moss balls in Ethiopia. Photo by Henk Greven, with permission.

At Tierra del Fuego, giant balls of *Racomitrium lanuginosum* form (Figure 33). Similar *Racomitrium* balls or hummocks form in Iceland (Figure 34). Examination of their interior revealed large clumps of grass. The *Racomitrium* had completely overtaken the grass.



Figure 33. These giant moss balls of *Racomitrium lanuginosum* have formed in the Tierra del Fuego. Could these be like the Iceland balls that form around clumps of grass, completely engulfing them? Photo by T. G. Allan Green.



Figure 34. *Racomitrium* hummocks in Iceland. Photo by Janice Glime

Wind and ice are not the only sources of creating moss balls. Action of waves can create similar assemblages (Figure 35-Figure 38). These strange assemblages of individuals have been reported from as distant places as Alaska (Iwatsuki 1976), Finland (Luther 1979), Japan (Iwatsuki 1956, 1977; Iwatsuki *et al.* 1983), and South America (Eyerdam 1967). Eyerdam found *Fontinalis* in balls up to 15 cm in diameter!



Figure 35. Moss balls of *Warnstorfia fluitans* var. *kutcharokensis* of Lake Kutcharo, Japan. Here moss balls are being made by wave action. Photo by Janice Glime.



Figure 36. Row of moss balls of *Warnstorfia fluitans* var. *kutcharokensis* along the shore of Lake Kutcharo, Japan. Photo by Janice Glime.



Figure 37. Moss ball of *Warnstorfia fluitans* var. *kutcharokensis* with arrows indicating green, growing apices. Photo by Janice Glime



Figure 38. Side branch typical of many of the stems in these *Warnstorfia fluitans* var. *kutcharokensis* balls, creating the dense structure that makes the ball. Photo courtesy of Zen Iwatsuki.

In shallow water near lake shores in Hokkaido, Japan, *Warnstorfia fluitans* (Figure 39) attaches to small rocks (Iwatsuki 1956); once the rock is dislodged, wave action rolls the moss back and forth, causing it to lie first in one position, then another, with any protruding branches being broken off (Iwatsuki *et al.* 1983). These growths become extremely dense. As the mosses reach shallower water, wave action is even greater. Ultimately they may be deposited in great numbers along the beaches. Stress causes the production of ethylene, and ethylene can result in short, wide cells under stress conditions in higher plants (Abeles 1973). This could partly explain the short, but firm, branches in the moss balls.



Figure 39. *Warnstorfia fluitans* growing normally. Photo by Michael Lüth, with permission.

Even animals can create moss balls. In the Dutch wetland forest, it is foraging pheasants that turn the mosses upside down and initiate the upward growth that creates the ball (Wiegers 1983). Although *Dicranum scoparium* (Figure 19) and *Mnium hornum* (Figure 40) formed such balls, other upturned wetland taxa did not.

Adaptive Significance

Often the life form is a passive response to exposure; any protruding individual is more subject to desiccation and hence has a shorter period in which to be active for photosynthesis, thus reducing its growth rate below that of its shorter but hydrated neighbors. Although this is more commonly known in cushions, Perez (1991) found that the same phenomenon occurs in moss balls of *Grimmia longirostris* (Figure 32) in the Venezuelan Andes. This spherical life form holds more water than the soil, and

larger balls hold more than small ones. In some cases, the form may be modified to accommodate the capture of cloud water or to avoid photoinhibition.



Figure 40. *Mnium hornum* forming cushion that could become a ball. Photo by Stepan Koval, with permission.

Mägdefrau (1935) found a clear relationship between life form and type of conduction. Dense tufts increase conduction, but there is considerable humidity difference within the tuft that suggests an important role in water retention (Zacherl 1956). When the air humidity is only 50% a few cm above the tuft, it can be as much as 90% within the tuft. Larger volumes are able to store more water, and volume increases more rapidly than surface area. Larger cushions have a greater volume of water per unit of surface area, thus losing less to evaporation than small cushions with a thinner boundary layer and greater proportion of surface area (Proctor 2000). Zotz *et al.* (2000) used *Grimmia pulvinata* (Figure 41) to demonstrate that the greater the size of the cushion, the more resistance it had to water loss. This size increase had no effect on the water-holding capacity on a dry mass basis, and the combination of these two factors contributed significantly to the length of the hydration period.



Figure 41. *Grimmia pulvinata* from southern Europe. Photo by Michael Lüth, with permission.

The cushion growth form (Figure 42) is important in decreasing the loss of water by reducing the turbulence of airflow (Figure 15). At low and even moderate wind speeds, the evaporative water loss from the cushion mimics that of a flat or rounded surface of the same area (Proctor

1984). This form is reminiscent of the tundra formations, where the cushions of seed plants not only impart resistance to moisture loss, but facilitate warming and protect from wind damage. The cushion shape presents a boundary layer that resists loss of moisture and permits wind to cross the plants with a minimum of disruption. Proctor (1979, 1980, 1982) found that the resistance to water loss extends the period of active metabolism after the precipitation stops. Nobuhara (1979) showed that *Bryum argenteum* (Figure 43) increased its water-holding capacity as the volume increased, with more than 100 shoots reducing the water loss to something very small.



Figure 42. *Leucobryum glaucum* cushions. Photo by Janice Glime.



Figure 43. *Bryum argenteum* in a large clump that helps to conserve water. Photo by Janice Glime.

The wind also can play a role in the formation of the cushion. As a branch, whether moss or tracheophyte, grows above the cushion, drying and wind action slow its growth and may even damage the terminal bud. Proctor (1980) demonstrated that when such surface irregularities reach the thickness of the boundary layer, there is a rapid increase in water loss at higher wind speeds. Thus, when a branch extends beyond the cushion, the other branches can catch up with it in growth before it is able to regain hydration and resume its growth, and if the terminal bud has been damaged, that growth may never occur.

Lewis Smith (1988) described the ability of dense turfs of *Schistidium antarcticum* (Figure 44) to hold strongly to their water content, but that the less densely packed shoots of cushions in xeric conditions could not maintain as high a water content as the turfs. Longton (1979a, b) drew a similar conclusion, noting that in Antarctica the plant size

decreases as the shoot density increases; the shorter, more compact growth form could be adaptive to the cold, relatively dry habitats.

Birse (1957) found that in some cases the growth form of certain species of bryophytes is almost invariable, whereas in others variation occurs according to the conditions of the habitat. Birse (1958a), reported that as long as there was a constant ground water supply, a variety of growth forms could flourish, especially tall turf and dendroid forms. In the absence of ground-water supply, short turfs, round mats, and one dendroid species (*Climacium dendroides*, Figure 45) were the only forms to survive.



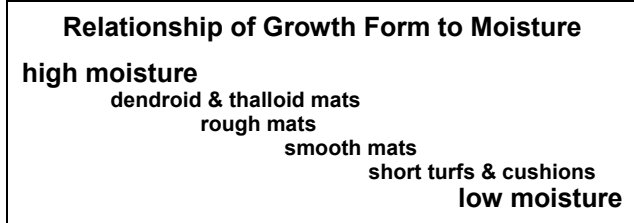
Figure 44. Growth of *Schistidium antarcticum* on Macquarie Island in the Antarctic. **Top:** The dense and well-hydrated turf surrounds *Ceratodon purpureus* growing in the crevices. **Bottom:** The uneven turf has exposed tops exhibiting dehydration. Photos courtesy of Rod Seppelt.



Figure 45. *Climacium dendroides*, showing dendroid growth form. Photo by Michael Lüth, with permission.

For endohydric mosses, growth form is important in water retention. Longton (1979a) found variations in the

seasonal growth patterns of *Hypnum cupressiforme*, and was able to relate these to water supply. Gimingham and Birse (1957) related growth form response to decreasing levels of moisture:



Dendroid mosses would seem to be particularly vulnerable to desiccation, with only a single stem in contact with the substrate and many exposed branches. Lorch (1931) found a correlation between the development of the central strand and the degree of branching, whereas the rhizome central strand became less developed, suggesting a greater importance for aerial water sources over soil sources as branching increased. Trachtenberg and Zamski (1979) supported these findings, re-affirming the importance of water absorption through the whole surface of the gametophyte and the utility of **apoplastic** transport.

Sollows and coworkers (2001) concluded that the colonial growth form of the leafy liverwort *Bazzania trilobata* (i.e. having branches lying on top of other branches; Figure 46) protected at least some inner shoots from the extreme exposures they experienced following clearcutting, avoiding the extinction of net photosynthesis observed in laboratory experiments following dehydration for 1-12 days. Likewise, it is likely that the overlapping leaves of this species afford additional water retention by creating capillary spaces.

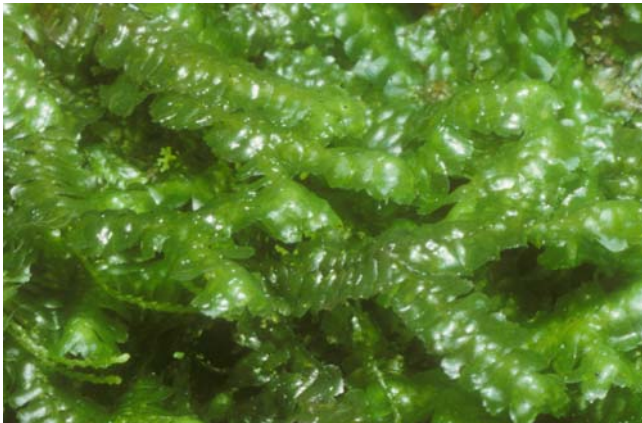


Figure 46. *Bazzania trilobata*, illustrating the overlapping nature of the branches and leaves. Photo by Janice Glime.

Nakatsubo (1994) compared growth forms in the subalpine region in Japan and found that xeric species were indeed often **large cushions**, as well as **compact mats**. Mesophytic species, on the other hand, comprised **smooth mats**, **wefts**, and **tall turfs** on the coniferous forest floor. He demonstrated that the evaporative rate per dry mass was indeed much less in the xerophytic cushions and compact mats than in the mesophytic forms. While the evaporative rate and dry mass were closely correlated with the growth form, the evaporative rate per basal area was not necessarily smaller in xerophytic taxa.

Matteri and Schiavone (1988) demonstrated that some taxa, e.g. *Polytrichastrum longisetum* and to a lesser extent *Bryum macrophyllum*, conserve their growth form but exhibit different life forms under different ecological conditions. During (1979) likewise related the growth form to the habitat. He found that *Campylopus flexuosus*, *Orthodicranum montanum*, and several other taxa form large turfs with almost no vegetative reproduction when living in moist, undisturbed environments, but when found in dry forests they consist almost entirely of dense cushions of easily detached branchlets.

But what empirical evidence do we have that the various growth forms and life forms actually afford any moisture advantage? Hanslin and coworkers (2001) demonstrated that increased shoot density of *Dicranum majus* (Figure 47) and *Rhytidiadelphus loreus* (Figure 48) actually had a negative effect on relative growth rate and green biomass, but that these were optimal at intermediate shoot densities in conditions of low relative humidity. It is likely that these species suffered a trade-off between light availability and moisture advantage at higher densities. In contrast, Bates (1988) found that *Rhytidiadelphus triquetrus* (Figure 49-Figure 50), likewise a boreal moss, had optimal growth when the colonies were most dense (1000 shoots dm⁻²) (Figure 50). Apparently in this case the dense packing of the shoots gives the advantage of reduced water loss and outweighs the disadvantage of reduced irradiance.



Figure 47. *Dicranum majus*, illustrating the dense colony that can reduce growth rate. Photo by David Holyoak, with permission.



Figure 48. *Rhytidiadelphus loreus*, a species that benefits from the moisture of dense clumps but grows less. Photo by Malcolm Storey <www.discoverlife.org>, with online permission.



Figure 49. *Rhytidiadelphus triquetrus* demonstrating loose and dry plants. Photo courtesy of Eric Schneider.



Figure 50. *Rhytidiadelphus triquetrus* demonstrating dense and moist plants. Photo by Janice Glime.

Habitat Relationships

Certain growth forms seem to fare best in certain kinds of habitats (Proctor 1990). In the absence of direct physiological evidence, we can use the observed field relationships to form hypotheses concerning the best life form strategies.

Deciduous Woodlands

Proctor (1990) suggests that **large size** and **rapid growth** are important for woodland and grassland bryophytes to permit them to grow above the litter and surrounding vegetation. This life form permits them the competitive life strategy. Moist, shady habitats are more favorable for **smooth mats** and **small cushions**, but larger taxa occur as well, taking advantage of nutrients in throughfall and exposing more surface area for photosynthesis. In her study of British deciduous woodlands, Birse (1958b) found that **wefts** and **mats** predominated, responding primarily to light as a determinant of abundance.

In humid, montane **tropical** forests, **pendant** and **fan** forms provide the most surface area for interception of the limited light without sacrificing moisture in this humid climate (Proctor 1990). Furthermore, they are able to trap water from mist and clouds. However, the great exposure makes them vulnerable to air pollution.

Pine Woods

Using Proctor's principles as a guideline, then what should we expect in a pine forest where leaf litter is a minimal problem? Seim *et al.* (1955) examined a Jack pine forest (*Pinus banksiana*) in Itasca Park, Minnesota, USA, and found **wefts** and **mats** as the predominant growth forms, with **cushions** and **turfs** comprising most of the remaining taxa. Gimingham and Robertson (1950) likewise found predominately wefts in Northern Britain. However, in another study, Moul and Buell (1955) found the turf type to be predominant (84%) in a sandy coastal pine woods of New Jersey, as did Hamilton (1953) in the hills of central New Jersey, USA. In alpine regions of Japan, Nakatsubo (1994) found that mesophytic species consisted of **smooth mats**, **wefts**, and **tall turfs** on the coniferous forest floor.

Epiphytes

Horikawa and Nakanishi (1954) developed a key to the "growth" (actually life) forms of Japanese epiphytic bryophytes. In it they included **small cushion**, **large cushion**, **turf**, **fascicular & shrubby**, **dendroid**, **simple feather**, **branching feather**, **mat**, **carpet**, **hardly pressed mat**, **loosely pressed mat**, **epiphyllous**, **pendulous**. They pointed out that species will vary with growing conditions, causing the same species to be assigned to more than one type.

Peatlands

Some terrestrial and peatland bryophytes may solve the CO₂ problem by a cushion or other dense growth form (*e.g.* *Sphagnum*) that provides CO₂ mostly from their own transpiration stream. In fact, *Sphagnum* seems to take advantage of CO₂ rising from deep in the peat, bringing up carbon stored there 1000 or more years earlier. Perhaps there is some advantage to having your living parts sitting on top of your dead parts!

Aquatic

Aquatic mosses such as *Drepanocladus vernicosus* rely on a water medium when submersed but benefit from close contact when emergent (Frahm 1978). Aquatic bryophytes are most constrained by CO₂. The **mat** form of *Nardia compressa* (Figure 51) and *Scapania undulata* (Figure 52) is beneficial in water below 0.1 m s⁻¹ where its leaf-area index permits it to exploit the low boundary-layer resistance of high velocities without incurring a high drag. On the other hand, the **streamer** form of *Fontinalis* (Figure 13h) provides the most exposure (maximum surface area) in relatively quiet water of less than 0.01 m s⁻¹ where boundary-layer resistance is high. Nevertheless, *Fontinalis*, with the same streamer life form, occurs in very rapid and turbulent water of mountain streams. Perhaps the turbulence itself permits enough CO₂ to mix with the water for the moss to take advantage of its greater surface area.

In the Antarctic, aquatic mosses showed the greatest plasticity when submerged compared to being grown in the air (Priddle 1979). *Warnstorfia sarmentosa* (as *Calliergon sarmentosum*; Figure 53) grew longer stems (longer internodes) and larger leaves in the water, whereas *Sanionia uncinata* (Figure 54) varied little from its terrestrial form.



Figure 51. *Nardia compressa*, a leafy liverwort with a mat growth form that reduces drag of high water velocity. Photo by Jan-Peter Frahm, with permission.



Figure 52. *Scapania undulata* showing flattened branches and leaves that reduce the drag of rapid flow. Photo by Michael Lüth, with permission.



Figure 53. *Warnstorfia sarmentosa* exhibiting short leaves and internodes in its exposed position above the water. Photo by David Holyoak, with permission.



Figure 54. *Sanionia uncinata* forming a thick mat. Photo by Michael Lüth, with permission.

Deserts

It is significant that Frahm (1978) found only 9% of the bryophyte flora of the Sahara to be pleurocarpous. In the moist boreal forest, pleurocarpous is the dominant form. Pleurocarpous mosses expose much more surface area to the drying atmosphere; rather, in the dry desert, **small cushions** and **wefts** (loosely interwoven, ascending shoots capable of growing out of the sand are better adapted to the dry and shifting substrate.

Polar Regions

Longton (1979b, 1982) followed the life forms that Gimingham and Birse (1957) attributed to the polar regions in attempting to compare the Antarctic to other polar areas. He considered four Arctic bryophyte habitats: wetlands, mesic communities, polar deserts, and bryophyte-dominated habitats. He considered wetlands to be dominated by the **tall turf** life form, with lesser representation of **short turfs** such as *Seligeria polaris* (Figure 55) on small stones.



Figure 55. *Seligeria polaris*, small, short turf moss on a pebble. Photo by Dale Vitt, with permission.

Mesic communities had a wider range of life forms than the wetlands, but the **tall turf** was still a dominant, with **short turfs** and **mat-forming** species also among the dominants. Although Longton (1979b) recognized five

habitat types among the mesic communities, these forms were generally common among all five mesic communities. However, in Iceland, the **weft** community joined the **tall turf** in prominence, along with mats of leafy liverworts. Furthermore, the birch woods there had abundant weft mosses.

Gimingham and Smith (1971) showed that the *Polytrichum strictum* (Figure 56) and *Polytrichastrum alpinum* (Figure 57) turfs lost water more slowly than *Chorisodontium aciphyllum* (Figure 58-Figure 59) and *Sanionia uncinata* in the same habitats, attributing this to the waxy cuticle on the former two. That *P. alpinum* loses only about 10% of its water when centrifuged suggests that most of its water is held internally compared to the 20% lost from *Chorisodontium aciphyllum*.



Figure 56. *Polytrichum strictum* forming cushions in Alaska; this species has a waxy cuticle that helps to maintain moisture. Photo by Andres Baron Lopez.



Figure 57. *Polytrichastrum alpinum*, a species in which surface wax helps to keep it hydrated. Photo by Europe 3 Michael Lüth, with permission.



Figure 58. *Chorisodontium aciphyllum* in Antarctica. Photo from Polar Institute through Creative Commons.



Figure 59. *Chorisodontium aciphyllum* in the Antarctic, a species that loses water more rapidly than its waxy counterparts.. Photo by Zicheng Yu through Public Domain.

The dry polar desert fellfields have **cushions** of both mosses and flowering plants, but other open areas have compact forms such as **mats**, **carpets**, and **short turfs** (Longton 1979b).

The bryophyte-dominated communities are those unsuitable for most tracheophytes (Longton 1979b). These include boulders, cliffs, musk ox dung, and hollows where snowmelt is late. The latter supports **large cushions** and **tall turfs** with small flowering plants rooted among them. The liverwort *Anthelia juratzkana* (Figure 60) is common here. **Small cushions** form on boulders, cliffs, and other rocky habitats. Rock crevices harbor **small mats** and **turfs**. **Large cushions** form on stony and marshy ground near permanent rivers and streams, with few bryophytes in the streams themselves. Where bryophytes do occupy streams, they are mostly **streamers** and **mats**.



Figure 60. Leafy liverwort, *Anthelia juratzkana*, forming black mounds on the soil surface. Photo by Michael Lüth, with permission.

The most unique of the polar habitats are those enriched with nitrogen by animal dung that support dense communities of dung mosses (**Splachnaceae**). Bird perches and lemming burrows support short turfs of acrocarpous mosses (Longton 1979b). Soil fractures between the polygons (Figure 61) support short turfs of cosmopolitan taxa such as *Bryum argenteum* (Figure 43), *Ceratodon purpureus* (Figure 44), *Funaria hygrometrica* (Figure 62), and *Marchantia polymorpha* (Figure 63).



Figure 61. Tundra polygons from freeze-thaw cycles showing bryophytes in the lower areas. Photo by Spencer & Carole, through Creative Commons.

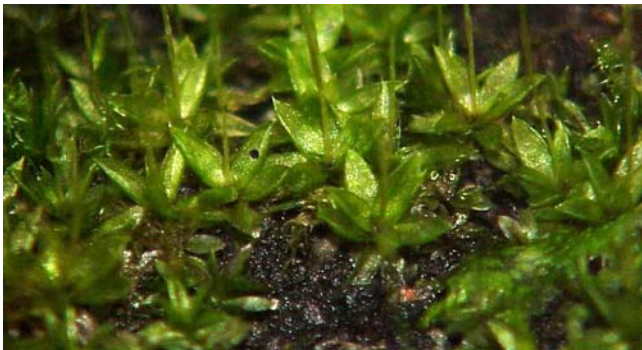


Figure 62. *Funaria hygrometrica*, a species that in the polar regions can live in the fractures between soil polygons. Photo by Kurt Stueber, through Creative Commons.



Figure 63. *Marchantia polymorpha*, a species that succeeds in the fractures between Arctic polygons. Image copyright by Stuart Dunlop <www.donegal-wildlife.blogspot.com>, with permission.

Racomitrium lanuginosum (Figure 33) forms extensive heaths resembling very large cushions in areas where it can gain water from the saturated atmosphere (Figure 34) (Longton 1979b). In areas with frequent precipitation as well as mist, *Sanionia uncinata* (Figure 54) forms moderately thick mats.

In the Antarctic, stones and gravel of nearly level ground support short turfs and cushions (Longton 1979b). In addition to these, calcareous substrata may have mats. Rock crevices have short turfs, small cushions, and mats.

Alpine

Alpine habitats seem to support mosses that resemble miniature tracheophyte growth forms. **Cushions** are common, but also **carpets** cover the dirt and provide protection from erosion. In studying the Ukrainian Carpathian Mountain alpine region, Ulychna (1970) included, in addition to these, bunches, dendroid, and interlacements, the latter two primarily in the transition into forest.

Studies Needed

While these growth and life form relationships to habitat seem to be well supported by field studies of species present, there has been little attempt to demonstrate that the proposed water relationships actually benefit the bryophytes. Transplant experiments need to be performed that compare the water loss of the various forms in a range of habitats, as well as their survival in this adult form without the need for surviving an establishment stage.

Summary

Growth forms are those genetically controlled characteristics of plants that determine their shape. These are manifest as **acrocarpous** with terminal perichaetia (including **protonema mosses** and **turf mosses**), **pleurocarpous** (**plagiotropic**, including **thread mosses**, **comb mosses**, and **creeping-shoot mosses**) with lateral perichaetia, **cladocarpous** with perichaetia terminal on lateral branches. **Life forms** encompass overall organization of growth form, branching pattern, general assemblage of individuals, and modification of a population by the environment.

The most widely used classification of **life forms** includes **annuals**, **short turfs**, **tall turfs**, **cushions**, **mats**, **wefts**, **pendants**, **tails**, **fans**, **dendroids**, and **streamers**. These can be subdivided, and a few others may exist in less well known habitats.

Growth forms and life forms of plants can aid in water retention by **reducing air resistance**, **increasing boundary layer thickness**, **providing capillary spaces**, and **protecting each other**. Thaloid forms protect one side of the plant at the expense of the other, but cuticular substances reduce the loss on the exposed side. Open growth forms (e.g. dendroid, rough mat, pendant) are more subject to water loss than compact, tight ones (e.g. smooth mat, short turf, cushion). The **cushion** form is able to provide the least surface exposure per unit of biomass and apparently has the lowest water loss rate. Conduction forms seem to

correlate with growth forms, with dense turfs increasing conduction as well as water retention.

Cushions and **moss balls** are formed as exposed shoots are broken off by force of wind, abrasion, and desiccation. Moss balls generally have a pebble at the center and arise in areas of wave action, wind on ice, solifluction (possibly), or other physical factors that tumble the moss.

Deciduous forests require large size and rapid growth such as wefts and mats to obtain enough light and avoid burial by litter. **Humid forests** support pendants and fans that can get moisture from fog and mist. **Pine forests** have wefts and mats, but also cushions, turfs, and smooth mats. **Epiphytes** include mostly appressed taxa such as smooth mats and small cushions, but a variety of other forms are possible in sufficient moisture. **Peatlands** take advantage of density to conserve moisture. **Aquatic** bryophytes are limited by availability of CO₂ and reduce the boundary layer resistance with **mats** or increase surface area with **streamers**. **Desert** mosses conserve water with small cushions and wefts. **Polar regions** support a variety of forms, depending on the habitat, with cushions predominating in habitats where tracheophytes also form cushions; turfs are common. **Alpine** bryophytes also benefit from the cushion form.

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CHAPTER 4-6

ADAPTIVE STRATEGIES: LIFE CYCLES

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CHAPTER 4-6

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Figure 1. Strap-shaped leaves of males and capsules with perichaetial leaves of females of the dioicous moss *Diphyscium foliosum*. Photo by Michael Lüth, with permission.

Life Strategies

By now it must be obvious to you that to understand the life strategies of bryophytes, one must first understand the life cycle (e.g. Figure 1). Frahm and Klaus (2001) state that bryophytes are able to react quickly to such events as climatic fluctuations because of their short life cycle and ease of dispersal by spores. It is likely that when all other plant life has perished from some Earth catastrophe, it will be the bryophytes that persist, surviving as spores or other propagules until conditions return to safety and once again surrounding the earth due to their ability to travel great distances as "dust."

By definition, the life cycle includes reproduction. However, even such a widely used term has ambiguities. In bryophytes, we shall use this term to refer not only to the sexual reproduction that results from union of sperm and egg (ultimately resulting in spores produced by meiosis), but also to the multitude of **asexual** (vegetative) means by which bryophytes are able to make more, physiologically independent plants (Mishler 1988). This definition separates reproduction, which can permit relocation, from

growth, which implies the increase in size of a physiological individual (Söderström 1994). On the other hand, growth can ultimately result in reproduction, as is the case when the plant branches and is physiologically connected, but later the branches separate and become physiologically independent. As you can see in Figure 2, the degree of reproduction by propagules depends on habitat. Among British habitats, short-lived habitats (wood, bark, farmland, dung) have the highest degree of propagular reproduction (that is, by vegetative means) (Herben 1994). On the other hand, the habitats with the greatest percent of the species are in the middle of the range of propagules.

Using the principle that extreme conditions might provide the best test of the limits of an organism, we learn that in the maritime Antarctic, bryophytes seem to have enhanced sexual reproduction (Lewis Smith & Convey 2002). This is contrary to the generally accepted belief that bryophyte fertility decreases toward the poles. Rather, 43% of the bryophytes (19 species) in Marguerite Bay and

47% of those on Alexander Island are known to produce capsules. But Lewis Smith and Convey attribute this to favorable microclimatic conditions. Nevertheless, in this extreme environment, the large majority of mosses with capsules were short, monoicous, acrocarpous taxa, suggesting that the predominance of dioicous taxa in more temperate climates may be possible because the environment is less stressful. In the more extreme environments of the Antarctic continent, the numbers of species producing capsules at similar latitudes (68-72°S) are much less (33%).

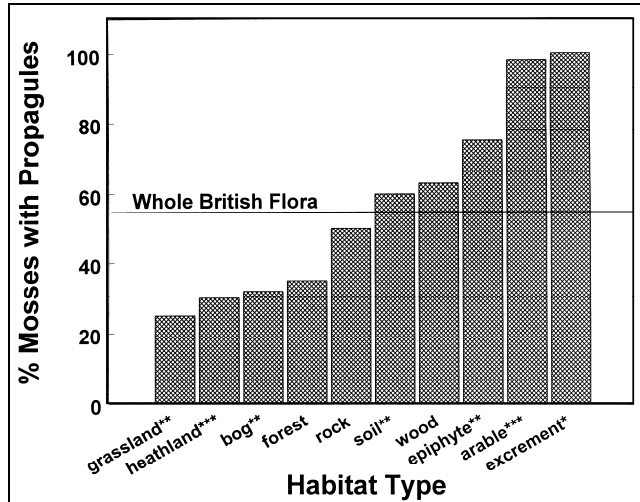


Figure 2. The percent of mosses that form spores or gemmae frequently or commonly in selected habitats of Great Britain. Asterisks indicate degree of significance (Chi-square test) when compared to the whole moss flora of Great Britain (* = $P < .05$, ** = $P < .01$, *** = $P < .001$). Redrawn from Herben (1994), based on data from Smith (1978).

Although life cycle strategies are obviously important, especially in extreme habitats, life forms and growth forms may be more important. During and Lloret (1996) found that within individual sites in Spain, species with the same life strategy exhibited similar patterns, and that between locations, growth forms differed more than life cycle strategies.

Clonal Growth

At the mature end of the gametophytic cycle, bryophytes can form masses of related individuals, or clones. **Clones** can be defined as groups of individual plants created by fragmentation, viviparous bulbils, or apomictic seeds (Callaghan *et al.* 1992), whereas if gene flow is present the groups of plants are called **populations** (Harper 1977). In other words, clones have the same genetic makeup as the plant from which they were derived. In addition to these tracheophytic means, bryophytes create clones through multiple buds on the protonemata. But, as already discussed, somatic mutations render even these "clonal" derivations to be variable in genetic makeup.

Callaghan, *et al.* (1992) attribute to clonal growth the ability to sequester space and increase fitness of the populations. Among the benefits are persistence; spread of development and reproduction over time and environmental conditions; risk-spreading between **ramets** (individual members of clone) of the same type, thus increasing chances for survival of the genotype; protection

of disadvantaged ramets that might later survive in the face of adversity; increased precision with the sequestering of space and dispersal of ramets; ability to monopolize resources for the benefit of the genotype. They furthermore include mobility, but I question whether this is much of a gain when compared to the alternative of wider distribution of propagules away from the parent.

One possibility that has barely been explored is the increase of genetic variability through production of these haploid genets. We had long assumed that the limited morphological development of the Bryophyta and Marchantiophyta reflected a limited genetic diversity, a case to be expected when the dominant generation is haploid and asexual reproduction is common. However, contrary to our expectations, moss populations are characterized by a high degree of isozyme variation, as shown for *Ceratodon purpureus* (Figure 3) (Shaw & Beer 1999). Cultivation of spores from one specimen of *Drepanocladus* (Warnstorfia) *trichophyllus* produced four distinguishably different morphologies (Sonesson 1966).



Figure 3. Color and leaf shapes of *Ceratodon purpureus*. **Top:** Green, broad leaf, hydrated form, **Middle:** Green, lanceolate leaf, hydrated form. **Lower:** Reddish dry form with capsules. Photos by Michael Lüth, with permission.

Velde and coworkers (2001) addressed this question of genetics of clonal relationships in *Polytrichastrum formosum*. They determined that identical genotypes between spatially separated shoots were almost never present, whereas identical genotypes among **genets** (branching of gametophytes resulting from clonal growth of rhizomes) was extensive. However, this view of the genet has some problems. Scrosati (2002) pointed out that somatic mutations are predictably common, giving rise to genetic mosaics within any connected genet. To deal with this lack of genetic homogeneity, Scrosati suggested that **genet** should be defined as a "free-living individual that develops from one original zygote, parthenogenetic gamete, or spore and that produces ramets vegetatively during growth." Nevertheless, it appears that even in adjacent populations of spore-producing plants, genetic variation is minor. In another example, populations of *Funaria hygrometrica* (Figure 4) growing in close proximity on contaminated tailings of a copper mine displayed very low levels of genetic variability, but had extensive morphological plasticity (Shaw & Bartow 1992).



Figure 4. Crowded *Funaria hygrometrica* with its abundant capsules. Photo by Michael Lüth, with permission.

During and van Tooren (1987) attempted to explain this paradox of genetic diversity in vegetatively reproducing taxa. Referring to earlier views of bryophytes as evolutionary failures, they contended that bryophytes in fact have high genetic variability, yet maintain their populations almost entirely by asexual means. They suggest that even though sexual reproduction, when it occurs, results in huge numbers of spores, establishment from spores in the field seems to be very difficult. Rather, they suggest that "remarkably rapid fine-scale dynamics" of many bryophyte populations may account for their ability to maintain a high degree of genetic variability.

Itouga and coworkers (1999) provide data on genetic variability in the liverwort *Conocephalum japonicum*. They consider both the species and populations to have low genetic diversity values of **Hes** (species genetic diversity) = 0.008 and mean **Hep** (population genetic diversity) = 0.008±0.003. Between populations diversity was likewise low with **Gst** (coefficient of genetic differentiation) = 0.062. They used this low diversity as an indication that reproduction by gemmae predominated over sexual reproduction by spores.

Velde and coworkers (2001) considered this strategy of producing clonal genets to be one that provided increased longevity for the genet that accompanies increased reproductive capacity. Nevertheless, they showed that male reproductive success in *Polytrichastrum*

formosum is determined primarily on spatial distance from females. In fact, these populations achieved their success primarily through sexual reproduction, facilitated by the ability of sperm to disperse to distances measured in meters rather than mm or cm.

Foraging and Sharing

The reproductive advantages of ramets may be enhanced by other advantages found more recently, at least in tracheophytes. In seed plants, the ability to relocate photosynthate from plant parts in the light to shaded parts has been demonstrated (Kemball *et al.* 1992), while other plants are able to translocate resources through rhizomes and roots (Landa *et al.* 1992). This permits the ramets to take advantage of flashes of sunlight called **sunflecks**, and horizontal growth that permits such advantages has been termed **foraging** (Bates 1998). Ramets furthermore may have seasonal advantages as different parts become exposed to light at different times of the year. Even nutrient and moisture advantages may accrue if part of the plant receives sunlight while another part extends into moister or more nutrient-rich soil. Even in simpler plants like lycopods (*Diphasiastrum flabelliforme*), Lau and Young (1988) demonstrated that ramets that had been severed from their connecting ramets experienced 50% more mortality than unsevered ramets. Those ramets connected to shaded ramets were able to maintain higher water potentials, giving them the ability to take advantage of the sun in one ramet while maintaining high water potential through that supplied by another ramet.

In bryophytes, as in tracheophytes, we can expect advantages to the clonal habit. Living where their parents have lived increases the probability that the habitat is suitable, thus reducing wastage of propagules. A greater area of soil and atmospheric water is contacted by a clone, in some cases permitting a greater nutrient capture and the opportunity to provide needed water and nutrients to the growing tip. However, the ability to transport hormones, nutrients, and photosynthate is known for so few examples of bryophytes that we cannot generalize these benefits. In some tracheophytes, leaves on different parts of the plant and within the clone differ in morphology, permitting different environmental conditions to favor them. Such differentiation may be possible on rhizomatous taxa such as *Climacium*, and some leafy liverworts exhibit different leaf morphologies on the same branch (e.g. *Lophocolea heterophylla*, Figure 5), but no systematic investigation has explored this as a possible clonal advantage.



Figure 5. Heteromorphic leaves of *Lophocolea heterophylla*. Compare the two leaves indicated by arrows. Photo by Janice Glime.

If indeed clonal transport such as that demonstrated in tracheophytes is possible in most bryophytes, nutrients could move internally from favorably placed ramets to those in less favorable positions in a patchy environment, benefitting the bryophytes in a competitive environment (Bates 1998). Bergamini and Peintinger (2002) likewise compared the bryophytes to tracheophytes, suggesting that their overall morphological responses to the differences in light levels approximated that of tracheophytes with stolons – a "spacer and branching strategy." But does this ability to share with less favorably placed ramets only work for bryophytes with internal conduction? Eckstein and Karlsson (1999) tested this hypothesis by comparing the movement of nitrogen in *Polytrichum commune*, with well-developed internal conduction, with that of *Hylocomium splendens*, with predominantly external conduction. Indeed, the labelled nitrogen pool in *Hylocomium splendens* moved from older segments to younger segments. In *Polytrichum commune*, it disappeared from younger segments in autumn, presumably going to underground storage organs. Both of these examples support the hypothesis that ramets can provide sources of translocatable substances from one part of the clone to another, but we have few studies to permit us to assess the extent of this phenomenon among bryophytes, nor does this explicitly demonstrate the transfer from one ramet to another less favorably positioned. And could gametophytes such as those in Figure 6 transfer substances from one gametophore to another through the protonema?

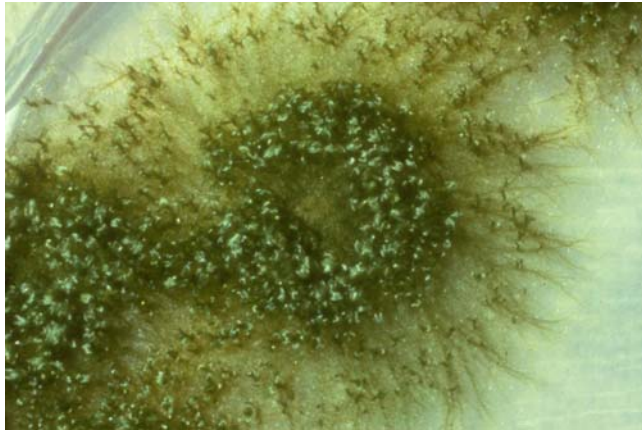


Figure 6. Circular growth pattern of gametophores developing from a single spore of *Funaria hygrometrica*. Photo by Janice Glime.

There need be no internal conduction to foster other types of advantages, however. For example, *Sphagnum magellanicum* is able to keep its neighbors moist through its efficient external conduction, and cushion mosses like *Leucobryum* (Figure 7) conserve moisture by growing in dense clones.

Implications for Reproduction

Perhaps there is a division of labor that provides a reproductive advantage among ramets of a clone that is independent of type of translocation. Stark *et al.* (2001) found that in the desert moss *Syntrichia caninervis* more mature ramets with larger size were more likely to reproduce than the smaller ramets, suggesting a division of labor that permitted smaller plants to conserve energy until they achieved a greater size. While this may be simply a

function of age, it would permit the colony to have multiple reproductive strategies simultaneously, with larger ones reproducing sexually and smaller ones using only fragments or vegetative propagules.



Figure 7. Cushion of *Leucobryum glaucum*. Photo by Janice Glime.

Many of the modes of reproduction of bryophytes result in clonal growth. Rarely does one see just a single bryophyte stem. Rather, clumps, cushions, tufts, mats, any number of growth forms, suggest that these are all siblings of an original single parent. In fact, even if only a single spore lands on the rock or soil, many plants arise, at least in mosses. The spore produces a protonema that branches, and in the case of the filamentous protonemata, the numerous branches can give rise to numerous upright gametophores. Knoop (1984) identifies two types of gametophore origin: *Funaria* type (Figure 6), developing gametophores on the caulonema only in a circular fashion around the spore; *Polytrichum* type, developing few gametophores near the germinated spore or even from the spore cell itself (Sood & Chopra 1973, Nehlsen 1979). Both result in several to many gametophores.

In *Sphagnum* a single spore produces a small thalloid protonema that gives rise to only one gametophore, thus resulting in populations when more than one spore germinates, and making one uncertain in any given clump of *Sphagnum* whether the clump is a clone derived from apical branching or a population derived from separate spores. However, if one considers that the branching of the **capitulum** contributes to a major portion of the mat growth, then, again, clonal behavior is at work. Furthermore, spores are likely to land on their own parents or siblings or cousins of the parent, and thus not be far removed from clonal relatedness.

Even gemmae can form circular arrangements of gametophores, as reported by Chopra and Rawat (1977) for *Bryum*, or other arrangements of numerous gametophores, as in *Physcomitrium sphaericum* (Figure 8; Yoshida & Yamamoto 1982). Since these have arisen from one parent, they likewise produce clones. In *Bryum bicolor*, numerous tubers and gemmae are produced early in the growth of the gametophore, permitting it to build up a large clone (Joenje & During 1977).

Density Effects

Colony density has varying effects on moss success. In ectohydric mosses, it is more likely that density will favor success and increase growth (During 1990; Økland & Økland 1996). But in *Sphagnum* (Clymo 1970) and *Rhytidiadelphus triquetrus* (Bates 1988) density is

detrimental to both branching and growth. Shoot mortality can increase, as in *Polytrichaceae* (Watson 1979), or decrease, as in *Tetraphis pellucida* (Kimmerer 1991), with density. Almost nothing is known of density effects on liverworts; Laaka-Lindberg (1999) showed that density had no effect on gemma production.



Figure 8. Clone of *Physcomitrium sphaericum*. Photo by Michael Lüth, with permission.

On the other hand, Kimmerer (1991), found that density was an important factor in asexual vs sexual expression in the acrocarpous *Tetraphis pellucida* (Figure 9). Gemmae were common in low-density colonies and the sex ratio was female-biased. High-density colonies, on the other hand, were more likely to have sexual reproduction and a greater proportion of males. She pointed out the advantage of this plastic strategy in unstable environments such as the rotting stump habitat of *Tetraphis pellucida*, permitting the plants to expand by gemmae when the colony was not dense.



Figure 9. *Tetraphis pellucida*. Upper: Uncrowded plants with gemmae on tips. Lower: Dense patch of plants with sporophytes. Photos by Michael Lüth, with permission.

Tradeoffs

Traditional life history theory holds that "maximizing reproductive value at each age is equivalent to maximizing fitness" (DeRidder & Dhondt 1992). However, in bryophytes, as in many species of seed plants, there is a negative correlation between sexual reproduction and asexual reproduction (Caswell 1985). On the other hand, in the clonal insectivorous flowering plant *Drosera intermedia*, DeRidder (1990) found only limited evidence of a tradeoff between the two types of reproduction. DeRidder and Dhondt (1992) suggest that traditional theory may apply to the clonal *D. intermedia*, whereas in many clonal species, it is an inappropriate theory because it was based on organisms (vertebrates) with only one mode of reproduction.

Ramets of one taxon, all from the same spore, seemingly competing for space and resources, seems like a maladaptive thing to do. However, the old safety in numbers adage may apply here. Multiple stems are less likely to dry out than a single plant. The colony can acquire a cushion shape as the middle members grow better due to moisture held by their neighbors. The edge members are slowed because if they too grow like the middle members, they are left with no protection from drought on the outer side. Hence, the adventurous stem that grows a bit taller is soon stopped by lack of moisture, and those on the edge are slowed the most because they lack a similar tall plant on the outside to protect them. For tracheophytes, Price and Hutchings (1992) also consider design constraints that limit vascular connections between some ramets, a consequence that should not be a problem for the ectohydric bryophytes. Could this, however, reduce the advantages for **endohydric** bryophytes, *i.e.* those relying significantly on internal conduction?

Perhaps one of the greatest benefits to ramets from a single spore of monoicous bryophyte taxa is availability of the opposite sex. Since in many cases, the male and female gametangia don't mature at exactly the same time on the same individual, gametangia of a neighbor are more likely to be receptive than other gametangia on the same plant. Such an opportunity is not so important to the tracheophytes because of their dependence on external pollinators that can readily visit nearby clumps of a different clone. Nevertheless, for the bryophytes, concomitant with the advantages of having nearby sexual partners are the tradeoffs in disadvantages of marrying your twin, in particular the loss of genetic diversity.

Like the tracheophytes, bryophytes must pay a price for the clonal habit. The advantage of being able to respond rapidly to environmental change is unlikely for the slow-growing bryophytes. Reduced recruitment from spores will make the clonal bryophytes vulnerable to permanent changes in the environment, and the connectedness makes the entire clone vulnerable to disturbance (*cf.* tracheophytes, Callaghan *et al.* 1992). The longevity of the clump in habitats like the Arctic make the probability of frost heave damage an eventuality in some habitats. Mosses seem less likely than tracheophytes to reap benefits from having only part of the clone disturbed. If part of a cushion is removed, the entire cushion is likely to dry out, whereas an intact cushion is able to keep its interior moist under most circumstances. In most cases, spread by spores in less clonal species may be a better

strategy, particularly for those that require fresh soil in open, disturbed areas. Thus, as their habitat changes, they have the means to move on to other suitable areas.

The trade-offs and benefits of clonal growth, contributing to increased bryophyte density, are hard to assess. The overwhelming presence of clonal growth suggests that it has its advantages for bryophytes, perhaps almost completely in the greater moisture retention.

r & K Strategies

Life cycles are basic to the survival of a species. Those that are annuals must usually survive the winter as spores. Those that are perennial must have other ways to survive the cold of winter. Still others may live where it is a dry season, not winter, that must be reckoned with. These differences in seasonal stresses are generally met by differences in life strategies.

Ramensky (1938) described three types of outcomes to the differences in life strategies as **violents** (aggressive species), **patients** (tolerant species), and **explerents** (non-competitive species that fill the spaces between others). Rabotnov (1975) added **pioneers** (species able to colonize substrata that are not yet suitable for other species). Meanwhile, MacArthur and Wilson (1967) introduced the concept of **r and K selection** as the extremes of a life cycle strategy continuum, and the western world seemingly ignored Ramensky and Rabotnov, generally only using the term "pioneer" among these. Although r and K strategies were largely described to fit animal concepts, many of the ideas can be applied as well to plants.

The **r-selected species** are characterized by a rapid growth rate, early reproduction, numerous, small offspring (spores or seeds in plants), and a high resource uptake; the **r** can be compared to the **r** (intrinsic growth rate) in the **logistic population model**. The **r strategist** is likely to be a short-stayer, adapted to disturbed or **ruderal** (field & wasteland) habitats where it is necessary to arrive quickly and mature before the habitat changes. By contrast, the **K-selected species** is characterized by slow growth rate, late reproduction, few, large offspring, and efficient use of resources; the **K strategist** optimizes for a high population density at the environment's carrying capacity (*cf.* the logistic model). The K strategist is likely to grow where the habitat is more stable, and it can be a long-stayer, eventually reaching considerable size (or cover). The K strategist is more likely to depend on asexual reproduction such as rhizomes and perennial habit whereas the r strategist is more likely to rely on seeds or spores and an annual habit with good dispersal.

Thus K strategists tend to be competitors; r strategists tend to be opportunists but not competitors. An r strategist is the more likely one to succeed on unstable, disturbed environments (sometimes a pioneer, sometimes an explerent), whereas the K strategist is the more likely one to succeed in more stable and predictable habitats (the patient or tolerant species and sometimes the violents or aggressive species).

Grime (1977) considered the **r strategist** to be **ruderal** (of field or wasteland) species that took advantage of disturbed habitats (Figure 10). The **K strategists** he considered to be the **stress tolerators** that were able to survive dry or cold periods as whole plants, the **perennial stayers**. Between those two he placed the competitors.

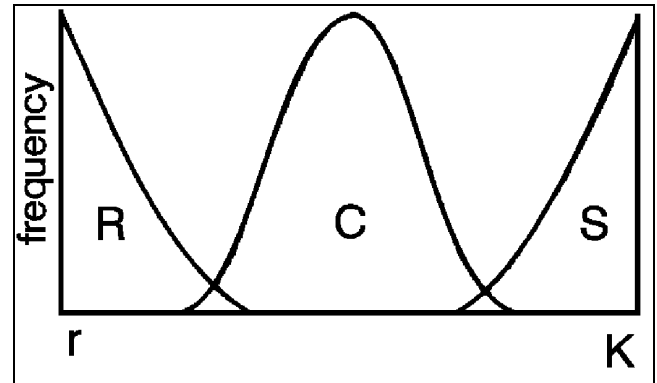


Figure 10. Frequency of ruderal (R), competitive (C), and stress-tolerant (S) species along an r-K continuum. Redrawn from Grime (1977).

Bet Hedgers

But between these two extremes are lots of possibilities for having some of the characteristics of each. Few species can meet all the criteria of either, and trade-offs abound to permit the organisms to meet the demands of their particular habitats. Plants that seem to have both good sexual reproduction and a means of vegetative reproduction are **bet hedgers**. Like the people to whom we refer as bet hedgers, these plants are "unwilling" to put "all their eggs in one basket." They use two strategies simultaneously so that they do not lose entirely. The price they pay is that they likewise never win entirely – at the ends of the spectrum, there is either an r strategist or a K strategist that is better adapted to the circumstances.

Production of gemmae among sexually capable species is one example of bet hedging. In the dry interior of North America, *Syrrhopodon texanus* (Figure 11) exhibits seasonal production of gemmae, arising in August (33% of specimens) and climaxing in September (50% of specimens) (Reese 1984). In this species, rarity of males makes this bet hedging a desirable strategy, although sporophyte-bearing females invariably occur when males are present.

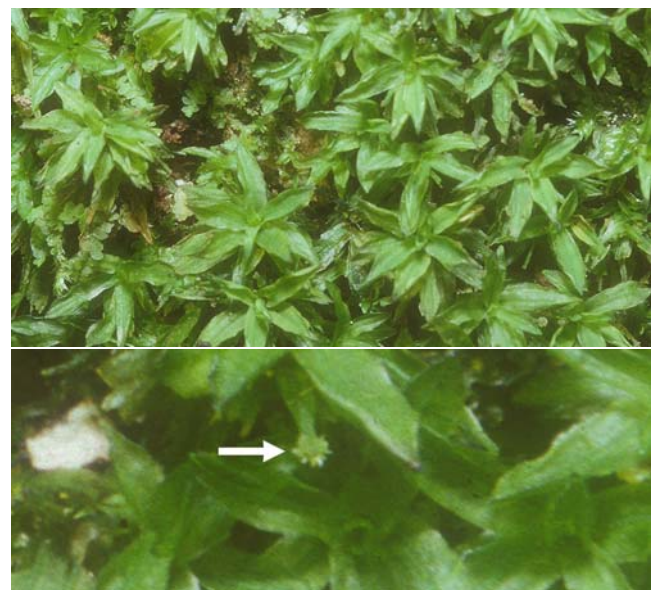


Figure 11. Gametophytes of *Syrrhopodon texanus*. Arrow in lower picture indicates gemmae at leaf tip. Photo by Janice Glime.

Dedifferentiation Issues

It is somewhat difficult to consider bryophyte r and K strategists in the same way as that of seed plants. These two strategies rely heavily on three characteristics of the plant life cycle: arrival and persistence, establishment and growth to maturity in a developing community, and time taken for the species to reach critical life stages (During 1992). Bryophytes are problematic because they do not follow a consistent pathway from spore (propagule) → juvenile → immature individual → reproductive individual. They can revert, growing from a fragment into an adult, or growing from a broken tissue of a fragment into a protonema → juvenile → immature individual → reproductive individual. Bryophytes are able to **dedifferentiate** – return a cell to its embryonic (undifferentiated) state

Compared to most tracheophytes, most bryophytes would appear to be r strategists, utilizing many small progeny (spores) that travel great distances and having short life cycles, permitting them to move on to new locations easily. This may help to account for the widespread distribution of many bryophytes relative to that of seed plants. However, when compared to phanerogams, most bryophytes do not meet the requirement for rapid growth.

Since most species will fall between the two extremes of r and K, the first thing one must realize when trying to determine the r or K status of a species is that ascribing r or K must be done in the context of comparison. Thus, within bryophytes, both ends of the continuum exist, while most species have a mix of characters.

Although bryophytes typically produce large numbers of small spores, many taxa also can increase in numbers by stolons, rhizomes, and branching, qualifying them as K strategists, or long-term stayers. For example, Hedenäs and co-workers (1989) found that the invading moss *Orthodontium lineare* in Sweden had a high spore output, but that colonies had a clumped pattern that indicated strong neighborhood effects that permitted spread within a locality. Thus, within the bryophytes, as in tracheophytes, species can be divided into r and K strategists, but they are unlikely to meet all criteria of either, and many trade-offs exist (Stearns 1989). Instead, it appears that many of them are bet-hedgers, being prepared to take advantage of whatever comes along instead of being prepared with a single strategy.

To succeed, they must balance their energy expenditure between sexual reproduction and vegetative growth in a way that best permits them to survive. These strategies must of course be coordinated with their entire physiology and the methods by which each developmental stage is signalled.

The r Strategist

Like typical r strategists, bryophyte r strategists rely heavily on massive numbers, typically 50,000 per capsule, of small spores (10-15 μm) to get to a new location (Schofield 1985). For example, *Funaria hygrometrica* can arrive quickly on disturbed sites such as soil charred by fire or agricultural land. But should this be true in predictably disturbed sites such as flood plains? In flood plains one finds members of Archidiidae (Figure 12), a subclass of large-spored mosses, with spores usually 50-150 μm , large

enough to be seen without a lens (Schofield 1985). Here it would appear to be advantageous to stay put by producing large, long-lived spores (Söderström 1994). It is likely that this stay-put strategy is available to many mosses and liverworts through spore longevity in soil banks.



Figure 12. A floodplain moss, *Archidium alternifolium*. Photo by Michael Lüth, with permission.

The K Strategist

Our understanding of perennial stayers (K strategy) is limited by our ability to determine the age of an individual. To age a moss or liverwort is somewhat difficult because among the perennial ones, the bottoms typically die as the tops continue to grow. However, many mosses carry their own age markers (Hagerup 1935), as described in more detail in another chapter, much as trees can be aged by terminal bud scars while they are young. *Polytrichum* males can be aged by counting the number of splash cups along the stem, because a new year of growth will come from the cup in the following spring. Ulychna (1963) found *Polytrichum commune* with a mean age of 3-5 years, but dead parts in the hummocks ranged 15-17 years. Brunkman (1936) found *Hylocomium splendens* (Figure 13) up to 30 years old by counting the successive sets of branches that form like stair steps, each from a point near the apex of the old, but it is unlikely that the oldest parts were still live and functioning. Because most bryophytes do not require their lower parts to keep the upper parts of the plant alive, they could theoretically grow indefinitely in a location due to the growth of the tips. Such a phenomenon is approached in *Sphagnum*, which will continue to grow as long as the habitat remains suitable.



Figure 13. *Hylocomium splendens* showing stairstep branching used for aging the moss. Photo by Janice Glime.

Spores, however, are not the only stage in which r and K strategies might be applied. One could also expect that

there would exist a trade-off between numbers of male and female gametangia. Just as some trees, such as maples (*Acer*) can adjust the number of male and female flowers based on tree crowding, one might look for regulation of numbers of male and female gametangia. In their studies of tropical bryophytes, Cavalcanti Pôrto and Moto de Oliveira (Moto de Oliveira & Cavalcanti Pôrto 2001; Cavalcanti Pôrto & Moto de Oliveira 2002) found that development of gametangia was responsive to rainfall. In the moss *Sematophyllum subpinnatum*, the number of antheridia per perigonium was 8-20 while the number of archegonia per perichaetium was 3-26. For *Octoblepharum albidum* (Figure 14) mean number of antheridia per perigonium was 13.4 and of archegonia per perichaetium 6.7. Could moisture regime change these ratios?



Figure 14. *Octoblepharum albidum*. Photo by Michael Lüth, with permission.

Just how do the r and K strategies of bryophyte gametangia line up? Fuselier and McLetchie (2004) considered this problem in *Marchantia inflexa*. They found that females had a greater growth rate, but males had more asexual reproduction. Males were also more likely to be present in a high light regime (55% shade), where they began sexual development earlier; males in low light produced no sexual structures (McLetchie *et al.* 2002). Fuselier and McLetchie (2004) postulated that eventually, the greater female growth rate would result in a population of all females as they overgrew males. However, under a disturbance regime, more males would be successful. They found a female bias in sex expression, with many genetically male plants failing to express sexual traits.

The r and K strategies are at best a continuum. Individual species often do not meet the criteria completely. Evolution is imperfect and time is required to drive it toward perfection. Furthermore, the model predictions work only if the environment perfectly matches with the set of bryophyte characters predicted. In the Antarctic, extreme conditions would seem to test this r and K continuum to its limits. And there the imperfections of these predictions are evident. The disturbed nature of this volcanic habitat favors r-selected taxa that must arrive from considerable distances (Convey & Smith 1993). However, the difficulty of spreading during the short, cold growing season favors certain short-lived taxa with large spores. Five of the species that are widespread in the Antarctic have large numbers of small spores and are most likely long-distance colonists. Even the longer-lived taxa seem to defy the r & K model predictions, having a large investment in sexual reproduction.

Life Cycle Strategies

To combat all the insults of the environment that might be encountered in a global array of habitats and climates, a variety of strategies exist among both plants and animals. For bryophytes, the predominant controlling factor is available moisture, but we must consider that temperature is also a major contributor to the timing of life cycle events.

As we consider the life cycle strategies of bryophytes, we must keep in mind that they potentially expose all of their alleles to expression and selection through a considerable portion of their lives – as *ln* gametophytes. All the variety in strategies discussed above come into play in permitting these tiny organisms to occupy the widest array of conditions of any group of plants. For the greatest number of species to survive across the greatest number of habitats, some have adapted to be **opportunists**, constantly moving from place to place, while at the other extreme are **perennial stayers**, finding a suitable place and remaining there for a long time. But because an individual bryophyte must stay in one place, it must have a life cycle that permits it to survive the onslaught of environmental fluctuations during the entire time it develops from protonema to leafy plant to fertilization to sporophyte to dispersal of spores.

The environment thus provides the major selection pressure on the life cycle strategies. Recognizing the instability of the environment, Stearns (1976) classified the environment into three main types (examples are mine):

1. having **long cyclic fluctuations**, with a period much longer than that of the generation time of the organism (*e.g.* fires)
2. having **short cyclic fluctuations**, with a period that is as long as or shorter than the generation time of the organism (*e.g.* seasons)
 - a. cycle highly predictable
 - b. start of cycle unpredictable
 - c. start of cycle predictable, but conditions of growing season unknown
 - d. start of cycle predictable, but conditions only partly known
3. having **random fluctuations**, *i.e.* not predictable (*e.g.* flash floods)

To survive in a fluctuating environment, the life cycle must prepare the bryophyte for the fluctuations. This means that at times it is advantageous to "run for your life" to other locations (produce spores), whereas under other, more favorable conditions it is best to sit still and keep your family together (reproduce vegetatively).

During (1979) has examined in detail the life cycle strategies of bryophytes in dealing with environmental conditions. In finding that most tracheophyte life cycle strategy systems either did not apply or were incomplete for the bryophytes, he devised a system of six strategies. He considered that bryophytes utilize three major trade-offs: few large spores vs. many small spores, survival of stressful season as spores (**avoidance**) vs survival as a gametophyte (**tolerance**), and life span that is negatively correlated with reproductive effort (for tolerants only) (During 1992). In addition, there is a usually tradeoff between sexual and asexual reproduction (Schofield 1981, During 1992). These considerations resulted in his organization of strategies based on life span, spore number and size, and reproductive effort (Table 1 and figures from During 1992; table slightly modified):

Table 1. Spore and life span characteristics of the various life cycle strategies for bryophytes as defined by During (1979).

Potential life span (yrs)	Spores		Repro effort
	Numerous very light <20 µm	Few large >20 µm	
<1	Fugitives	Annual shuttle	High
Few	Colonists		Variable
	Ephemeral	Short-lived shuttle	
	Colonists	Long-lived shuttle	
	Pioneers		
Many	Perennial stayers	Dominants	Low
	Competitive		
	Stress-tolerant		

The system of During has attributes that work as well for higher plants, and Frey and Hensen (1995) have proposed a modified system based on this one to be used for all plants. (Now how often do you see those tracheophyte folks copying a bryophyte idea?! Kudos to During!) They have expanded upon the original six strategies proposed by During to include nine: annual shuttle species, fugitives, kryptophytes, short-lived shuttle species, colonists, perennial colonists, perennial shuttle species, perennial stayers, and perennial stayers with diaspore years. Hürschner and Frey (2012) included geophytes and perennial shuttle species to the bryophyte list.

Fugitives (Figure 15), **colonists** (Figure 16), **annual shuttle species** (Figure 17), and **short-lived shuttle species** (Figure 18) are **r strategists** and all succeed in disturbed environments. The fugitive strategy is relatively rare, with *Funaria hygrometrica* being one of the few examples (During 1992). That many species require disturbance and therefore are relatively rare in any specific locality is usually overlooked in trying to conserve rare taxa. The very disturbance they need to persist is often prevented in an effort to maintain them! Noble and Slatyer (1979) attribute success following disturbance to plant strategies related to three factors: method of arrival (fugitives, colonists, annual shuttle species) or persistence at disturbed site (short-lived shuttle species); ability to become established and reach maturity in disturbed site; time needed to reach critical life cycle stage. These criteria are not intended to include those of taxa adapted to continuously disturbed or catastrophically disturbed habitats, but rather to those recurring events such as fire, flood, or treefall. The **perennial** bryophytes are **K strategists** (Figure 19, Figure 20) of stable habitats.

During (1992) added the category of **dominant** to accommodate taxa with large spores and long life expectancy, such as some *Sphagnum* species. It is a rare combination among bryophytes, whereas it is relatively common among trees. Other categories will surely be added as we gain understanding of tropical ecology and the adaptive strategies of bryophytes there (During 1992). One such category could develop based on **neoteny**, where juvenile characters are retained in adults, a condition that occurs among some species of ephemeral habitats such as living on leaves in the tropics (During 1992). In some taxa, such as *Buxbaumia*, neoteny permits the species to avoid some life cycle stages, in this case the leafy gametophyte! La Farge-England (1996) has suggested the category of **protonema mosses** to encompass these few taxa (see chapter on life forms and growth forms). Others, such as

Dicranum and *Fissidens* species, have **dwarf males** that develop on leaves of female plants, facilitating the transfer of sperm to the egg, a kind of male neoteny. (See chapters on sexuality and on the development chapter on gametogenesis for further discussion of dwarf males.)

Diaspore Banks

Disturbed habitats, whether the product of predictable natural phenomena or unpredictable events such as human intervention or volcanic eruptions, benefit from the bank of spores and asexual **diaspores** (any structures that become detached from parent plant and give rise to new individuals) stored in the soil out of reach of sun and sometimes even water. Major disturbances can bring these propagules to the surface where they can break dormancy and become established. We need only look at a recently disturbed bank in a forest, sloping deforested hillside, or crumbling streambank to recognize the importance of bryophytes in colonizing and often maintaining the surface integrity. Yet, as Ross-Davis and Frego (2004) pointed out, while these regeneration processes "may be critical to conservation of severely disturbed communities..., they are poorly understood." In an attempt to quantify this importance they sampled two grids in managed Acadian forests of New Brunswick, Canada. They identified 51 taxa in the aerial diaspore rain and buried diaspore banks. Of these, 36 represented species in the existing community of the Acadian forest. The composition of aerial diaspores was more similar to the existing community than to that of buried ones.

Tradeoffs

For bryophytes, the system of success strategies is complicated by the ability to reproduce from fragments, and in many cases the production of asexual propagules on the protonemata as well as on the leafy plant, leading During to his 1992 revision. One must keep in mind that bryophytes may be among the best dispersers in the world. Therefore, large spore size, as opposed to small ones with worldwide dispersal potential, may be a tradeoff of great magnitude. While many of these small spores will not survive the long distance travel due to UV radiation and other atmospheric hazards (see dispersal chapter later), many will survive significant local travel, with a few travelling for hundreds of kilometers.

Once the spores arrive, different attributes become important. The spore must have sufficient energy to survive until favorable conditions arise, and it must get the new protonema off to a good start with enough energy to survive in some very harsh environments. This has resulted in a correlation of spore germination patterns with habitat (Nehira 1987). Epiphytic and saxicolous species of both mosses and liverworts tend to have **endosporic** germination (*i.e.*, early development of several mitotic divisions within the spore wall; Figure 21), permitting them to be multicellular when they emerge from the protection of the spore. This would suggest that these species carry sufficient nutrients with them to supply their initial developmental nutrient needs. On nutrient-poor, **xeric** (dry) substrates such as rock and bark, internal development could insure protection during early, critical stages of development. However, most mosses have **exosporic** germination (first mitotic division occurs outside spore after rupture of spore wall).

Life Cycle Strategies based on During (1979, 1992)

Fugitives

Fugitives – species that live in unpredictable environments

example: *Funaria hygrometrica*

short life span; ephemeral or annual

high sexual reproductive effort; large percent of plant devoted to spore production

low age of first reproduction (first year)

spores small (<20 μm), very persistent and long-lived

no asexual reproduction

innovations absent

open turfs

rare in phanerogams (mustards?) and bryophytes; found among bacteria, algae, fungi

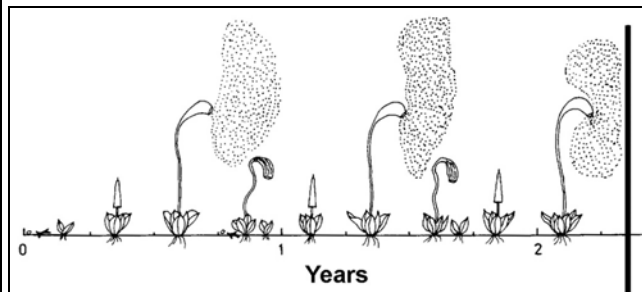


Figure 15. Fugitive strategy. From During (1979).

Colonists

Colonists (*sensu stricto*) – species that live where habitat start is unpredictable, but lasts several years; secondary succession

bryophyte examples: *Bryum bicolor*, *Bryum argenteum*, *Ceratodon*, *Marchantia*

short life span; (annual-) pauciennial-pluriennial

sporophyte late, somewhat rare in many; first sexual reproduction at least after 1 and usually 2-3 years

high reproductive effort

spores < 20 μm , persistent

innovations present

asexual in early life; first asexual reproduction in a few months

usually short turf

old field species like *Solidago*

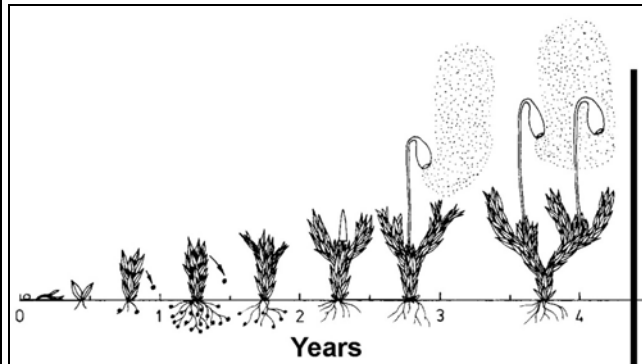


Figure 16. Colonist (*sensu stricto*) life cycle strategy. From During (1979).

Colonists

Colonists (ephemerals) – gap-dependent species

bryophyte example: *Bryum erythrocarpum*

short life span; (annual-) pauciennial-pluriennial

first sexual reproduction in a few months

sexual reproduction rare

spores < 20 μm , persistent, numerous

high asexual reproductive effort by subterranean tubers on rhizoids

river flood plains, low areas submerged in spring, cultivated fields

usually short turf

Colonists (pioneers) – species that live where habitat start is unpredictable and habitat lasts at least several years after disturbance; make habitat suitable for perennial stayers (Rabotnov 1975)

bryophyte examples: *Grimmia*, *Schistidium*

long life span

slow growth

perennial

high reproductive effort

first sexual reproduction in a few years???

sexual reproduction low

asexual reproduction high

spores < 20 μm , persistent

river flood plains, low areas submerged in spring, cultivated fields

usually short turf

Shuttles

Annual Shuttle – species that require small disturbances that last 1-2 years; survive severe stress periods

bryophyte examples: *Ephemerum*, *Physcomitrium*, *Fossombronia*

short life span; (ephemeral-) annual-pauciennial

sexual reproduction effort high and frequent

age of first reproduction < 1 year

spores large, 25-50 (-200) μm

survive by spores

capsules often immersed (short or no setae) (Longton 1988)

specialized asexual reproductive structures absent

innovations rare

open turf or thalloid mat

agricultural weeds, hoof prints, steep stream banks, dung

disturbed habitat species like *Brassica*

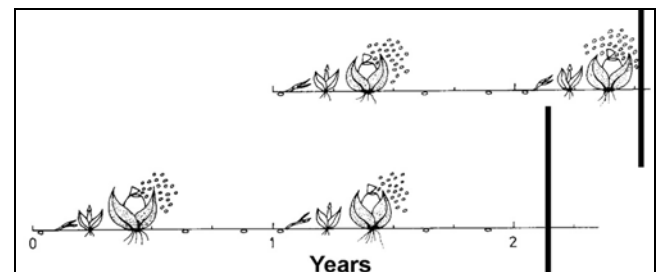


Figure 17. Annual shuttle life cycle strategy. From During (1979).

Short-lived Shuttle – species that don't avoid periods of severe stress; habitat lasts 2-3 years
 bryophyte examples: *Hennediella heimii*, *Splachnum*, *Tetraplodon*
 life span several years, pauci-pleuriennial
 sexual reproductive effort high; sporophytes more or less frequent
 overall reproductive effort medium
 ages of first reproduction 2-3 years
 spores large, 25-50 (-100) μm
 asexual reproduction rare
 innovations present
 short turf or thalloid mat

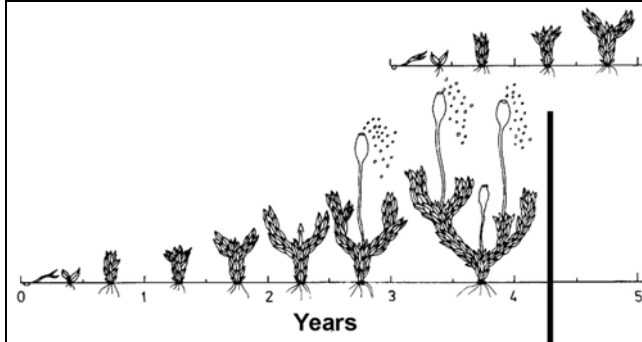


Figure 18. **Short-lived shuttle** life cycle strategy. From During (1979).

Perennial (Long-lived) Shuttle – species that require stable environments, such as epiphytes, where end of habitat is predictable
 bryophyte examples: *Orthotrichum*, *Marchantiales*
 long life span; pluriennial, perennial
 sexual reproduction effort moderate (During 1979) or low (During 1992)
 age of first sexual reproduction high (>5yrs)
 spores large (25-200 μm)
 spore life span short
 asexual reproduction effort moderate
 innovations present
 age of first asexual reproduction variable
 cushion, rough mat, smooth mat, tuft
 tracheophytes include bromeliads, *Betula*, *Populus*

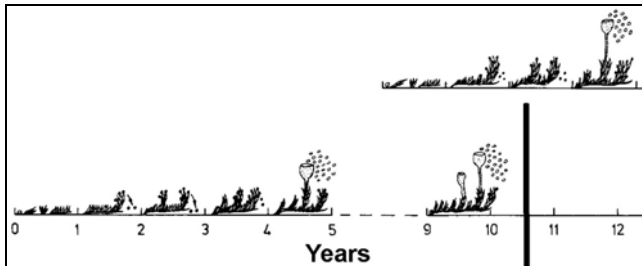


Figure 19. **Perennial long-lived shuttle** life cycle strategy. From During (1979).

Perennial Stayers

Perennial stayers (competitive) – forest floor
 bryophyte examples: *Brachythecium rutabulum*
 long life span
 perennials
 rapid growth
 sexual and asexual reproduction low or nearly absent
 age of first reproduction several years
 spores <20 μm
 spore longevity variable
 wefts, dendroids, mats, large cushions

Perennial stayers (stress-tolerant) – fens, bogs, desert

bryophyte examples: *Sphagnum*, *Syntrichia ruralis*
 long life span; perennials
 slow growth
 sexual and asexual reproduction low or nearly absent
 age of first reproduction several years
 spores <20 μm
 spore longevity variable
 growth form plasticity
 in deserts include acrocarpous taxa with long setae
 tracheophytes include ericaceous shrubs

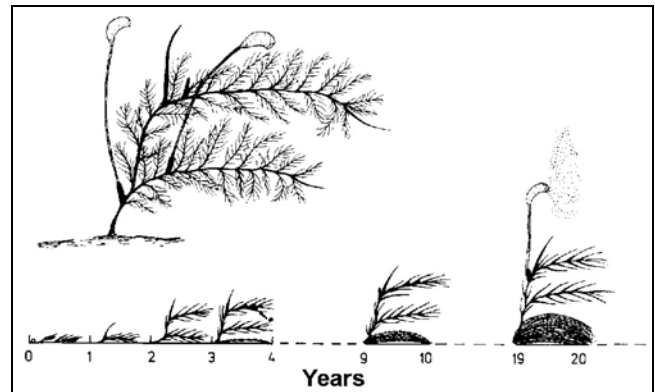


Figure 20. **Perennial stayer** life cycle strategy. From During (1979).

Dominants – bogs

bryophyte example: some *Sphagnum*
 long life span; perennial
 sexual reproduction effort low
 spores large (>20 μm)
 asexual reproduction effort low
 turf

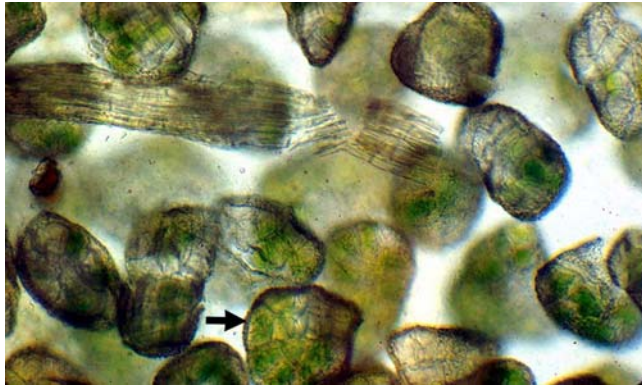


Figure 21. Endosporic development (arrow) in spores of the hornwort *Dendroceros tubercularis*. Photo courtesy of Karen Renzaglia.

But spores are not the only way to travel. Fragments and propagules can carry the species to a new location, although the generally much larger size would usually limit distance considerably. Moss balls (see chapter on life form) along lake shores and on glaciers and snow banks serve as means of dispersing large units, including multiple plants. Landslides, rock movement in streams, trampling, and vehicle tires can carry fragments for some distance. For those producing asexual propagules, sexual reproduction and asexual propagules are usually not produced at the same time. Thus, investment in specialized asexual structures is indeed a trade-off. Taxa with annual life cycles, surviving unfavorable conditions as spores, rarely produce such specialized structures, investing their energy instead in the production of spores (During 1992).

We know little about the energy costs of producing spores and other propagules, and in particular know nothing of the effect of spore production on mortality (During 1992). There is evidence, however, that development of sporophytes slows the growth of the gametophytic plant in *Scorpidium scorpioides* (A. M. Kooijman & H. J. During, unpubl. data) and *Plagiothecium undulatum* (Figure 22; Hofman 1991), as well as in *Dicranum polysetum* mentioned earlier (Bisang & Ehrlén 2002). This tradeoff may be a general rule, as discussed in the chapter on sporophyte development.



Figure 22. *Dicranum polysetum* exhibiting its multiple setae per stem. Photo by Janice Glime.

Some characteristics of the life strategies may be interrelated. For example, Hedderson (1995) found that in the Pottiales the probability of producing capsules decreased with increased life expectancy and was negatively associated with asexual propagules. As discussed in the chapter on asexual propagules (brood bodies), these compete for energy with the production of capsules and generally do not occur simultaneously. It therefore follows that dioicous taxa in this group have more asexual propagules, corresponding with their lower likelihood of having sexual reproduction. Unlike sporophytes, asexual propagules were positively associated with life expectancy. On the other hand, size accounts for only a small, but statistically significant, proportion of the variation in life history traits in the Funariales, Polytrichales, and Pottiales (Hedderson & Longton 1996). Rather, characteristics related to water relationships were most important, accounting for 40-50% of the variation. It is interesting that the ability to take in and retain water coincides with monoicous taxa that are short-lived and produce few large spores, whereas those at the opposite end of the endo-ectohydric gradient have opposite characters. Spore number and spore size are strongly related to family, with most of the variation occurring among genera. Variation among species is moderate. Hedderson and Longton suggested the possibility of coevolution of water relations and life history in these orders.

Longton (1997) used the concept of life history strategies to predict character relationships. Colonists, fugitives, and shuttle species exhibit an earlier age for first reproduction as the longevity decreases. These strategies are accompanied by greater monoicy and reproductive effort (Longton 1997, 1998). Such species tend to have more plastic phenotypes and experience greater success at establishment by spores. Dioicous moss colonists, on the other hand, are more likely to produce asexual propagules, whereas such propagules are widespread among liverworts.

Generation Time

Generation time is one of the contributors to life cycle strategy, but we have no comprehensive study by which to label this function for bryophyte species in general. In order to meet the IUCN red list criteria, bryophytes must be put into generation time categories. This is important because environmental changes may take longer to affect numbers of those species with a long life cycle than for those with a short one. Tomas Hallingbäck (Bryonet 9 January 2014) reports that in Sweden they have used templates of 10, 20, 50, and 100 years as the intervals for three generations. Since hard data are generally not available, the Swedes agreed upon approximate generation lengths and life spans and classified their species based on the potential life span of the gametophyte:

- 'short' (colonists s. str., fugitives) = 3 generations = 10 (e.g. *Microbryum* spp.)
- 'medium' (pioneer colonists, short-lived shuttle) = 3 generations = 20 years (e. g. a typical epiphyte like a *Syntrichia*)
- 'long' (long-lived shuttle – perennial stayers) = 3 generations = 50 years (e.g. *Hylocomium splendens*).
- For species rarely found with sporophytes, a generation time of 25 years was recommended

Habitat Studies

Occasionally a habitat study will describe the growth forms or life forms that dominate there. But quantitative studies to describe these are rare. However, a few examples from tropical habitats can serve to provide an understanding of their usefulness in giving a mental picture of the bryophyte cover in places we have never visited.

In the **Colombian cloud forest**, epiphytes are abundant due to the high moisture availability from the clouds and the infrequency of desiccation events. This type of climate supports growths of tall turfs and smooth mats as predominant growth forms on the trees (van Leerdam *et al.* 1990). On the other hand, the life strategies of bryophytes on trees on the **eastern Andean slopes** of northern Peru reflect the drier habitat. Colonists form short turfs of acrocarpous mosses, primarily in secondary forests suffering disturbance. In the **lowland** and **submontane forests**, perennial shuttle species and perennial stayers exercise low sexual reproductive effort and take advantage of the high humidity to accomplish high vegetative reproduction through both propagules and clonal growth (Kürschner & Parolly 1998a). *Macromitrium* (Figure 23) and *Phyllogonium fulgens* (Figure 25) have dwarf males resulting from small male spores compared to large female spores. (Dwarf males are discussed more thoroughly in the chapters on sexuality and gametogenesis.) *Leptodontium viticulosoides* (Figure 24) exhibits functional heterospory in which small spores are dispersed long distances and large ones only short distances. On the other hand, at high elevations **near timberline**, the perennial shuttle and perennial stayer species instead exercise a high sexual reproduction and produce numerous sporophytes. Similar altitudinal differences occur in Southeast Asia and Central Africa.



Figure 23. *Macromitrium sulcatum*, member of a genus with small male spores and dwarf males. Photo by Manju Nair, through Creative Commons.

Bryophytes of the **tropical lowlands** have a very different character from these montane epiphytes, providing them with maximum water conservation in this much drier habitat. The mat life form encompasses species with water lobules, water sacs, and rhizoid discs (Kürschner & Parolly 1998b). This life form gives way to fans, wefts, dendroids, and pendants in the more humid

montane belt. These forms serve as collectors to condense water vapor from the frequent fog and mist (**fog-stripping**; Figure 26). Deeply fissured or ciliate leaves and rill-like arrangement provide the fine wire-like surfaces needed for this water capture. The **tropical orear** and **subandean belt** contrasts with this foggy area by having strongly contrasting diurnal conditions and supporting short-turf, tall-turf, and tail life forms with central strands, rhizoids, and rill-like leaf arrangements.



Figure 24. *Leptodontium viticulosoides*, a species that has functional heterospory. Photo by Li Zhang, with permission.



Figure 25. Pendant *Phyllogonium fulgens* in Japan. Photo by Janice Glime.



Figure 26. "Fog-stripping" by thin leaves of *Campylopus holomitrius* in the mist from geothermal vents at Karapiti, New Zealand. Photo by Janice Glime.

Bryophytes of **arid habitats** are typically small and may include acrocarpous perennial stayers with small spores and long setae that aid in dispersal (Longton 1988). Annual shuttle species here are primarily ephemerals that avoid desiccation by going dormant as spores, develop rapidly to maturity following rain, and produce large spores in capsules that typically lack stalks and remain submersed among the perichaetial leaves; often these capsules lack peristomes and opercula and may be dispersed as whole capsules (see chapter on development of sporophytes). The perennial shuttle species are mostly thallose liverworts such as *Riccia* (Figure 27) that curl up and become dormant or survive as large spores. Fugitives may arrive, but generally are gone after 1-2 years, travelling to new sites as small spores.



Figure 27. *Riccia sorocarpa*, showing curling leaves that facilitate survival of dry conditions. Photo from Botany website, UBC, with permission.

González-Mancebo and Hernández-García (1996) related life strategies to habitats along an altitudinal gradient in the Canary Islands. They found the following trends for the most abundant strategies:

higher elevations: colonists
rocks in driest forest: colonists, short-lived shuttle,
long-lived shuttle

humid forest trees: long-lived shuttle, short-lived shuttle
humid forest soil: perennials
soil in shady, dry forest: perennials

These strategies seem to be determined by humidity conditions, substrate dynamics, and vegetation disturbance. Not surprisingly, the perennial life strategy had the lowest percentage of fertile species. The other strategies typically have approximately 70% fertility.

Summary

Bryophyte life strategies must be closely attuned to the water regime of their environment. They accomplish this fine tuning by using spores, fragments, and specialized asexual propagules during times when conditions are not suitable for the gametophyte. Furthermore, they attune their times of sexual reproduction to meet the availability of water. Secondary to the water schedule is the advent of disturbance for which some bryophytes are especially adapted (**opportunists**).

Bryophytes, especially mosses, are clonal organisms. All bryophytes are able to spread vegetatively through fragments and propagules. Perennial mosses also spread by branching (**ramets/genets**). Mosses, additionally, produce many upright gametophytes from the protonema developed from a single spore. Clones have the advantage of maintaining moisture, but have the disadvantage of being genetically identical. Bryophytes that grow horizontally have been considered **foragers** that are able to take advantage of a patchy environment to obtain nutrients, light from **sunflecks**, and even water in different parts of the plant. They are able, at least in some taxa, to transport these nutrients or the photosynthate to other parts of the plant. Sexual reproduction is favored when clones and clumps provide both sexes, and even in monoicous taxa the differences in maturation times among members of the clone become an advantage.

Density can work for and against bryophytes. At low densities, water loss is greater and sexual reproduction is less successful, favoring spread by spores at high densities. However, in some mosses, such as *Polytrichum*, shoot mortality can increase with density, but in other taxa it can decrease.

There is a tradeoff between sexual reproduction and asexual reproduction, including branching and growth, as these events compete for energy.

Compared to tracheophytes, bryophytes are **r strategists**, but within the bryophytes there is an entire range from **r strategist** to **K strategist**. The **r strategists** rely on large numbers of small spores and a short life cycle (**opportunists**). **K strategists** rely on their clonal, perennial growth (**perennial stayers**) and often have only limited sexual reproduction or are strictly vegetative. But most bryophytes lie somewhere on the **bet hedger** line, producing spores sexually, but using fragments and asexual propagules during seasons when energy is not needed for sexual reproduction or spore production. Because of their ability to

dedifferentiate, bryophytes often spread by fragments of ordinary tissue.

Availability of water is the most important determinant of life cycle strategy. Endosporic development is more common on low water, low nutrient substrates like rock and bark. Disturbance is actually required for some species.

Bryophytes utilize three major tradeoffs: few large spores vs. many small spores, survival of stressful season as spores (**avoidance**) vs survival as a gametophyte (**tolerance**), and life span that is negatively correlated with reproductive effort. **Diaspore banks** permit bryophytes to survive untenable periods of time in a dormant state and begin growth when suitable conditions return. **Endosporic development** permits some bryophytes to get a head start in particularly short-lived periods of adequate moisture, such as deserts, floodplains, and vertical substrates.

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Jean Faubert caught some serious inconsistencies in the r-K selection text and made valuable suggestions to improve this subchapter.

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CHAPTER 4-7

ADAPTIVE STRATEGIES: VEGETATIVE VS SEXUAL DIASPORES

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CHAPTER 4-7

ADAPTIVE STRATEGIES: VEGETATIVE VS SEXUAL DIASPORES



Figure 1. *Marchantia polymorpha* showing both vegetative diaspores (gemmae in splash cups) and umbrella-like archegoniophores where sporangia and sexual spores are housed. Photo by Michael Lüth, with permission.

Diaspores

Diaspores are everywhere and some are ready to grow. In bryophytes, **diaspores** are spores and other propagules, including fragments, that function in dispersal (see Figure 1). These may be airborne, drop within the parent colony, or become buried in a diaspore bank in the substrate. Some even are dispersed by animals or water. They serve both to increase colony size and to invade new places.

Nevertheless, spread of many species is dispersal limited. Sillett *et al.* (2000) found that nine species of bryophytes had colonized branches of Douglas fir (*Pseudotsuga menziesii*) from 1995 to 1999, with relatively rapid colonization in all age classes. Nevertheless, when bryophytes were transplanted to Douglas fir trees, they became more frequent on inoculated branches than on ones not inoculated by the researchers. This suggests that these bryophytes were dispersal limited in colonizing the trees.

The importance diaspores is exemplified by the large number of bryophytes that occur on multiple continents.

Of the 7567 accepted binomials for liverworts and hornworts, 2211 are found on more than one continent (Anders Hargborg, pers. comm. 23 February 2017). And of these, 20 are found on all 7 continents plus Oceania. Frey and Hensen (1995) considered dispersal of such importance that they proposed a life strategy system based on dispersal strategies. One strategy that differed from other systems was the **perennial stayers with diaspore years**. That is, some years have prolific reproduction, vegetative or sexual, whereas in other years these are more limited.

Sampling Methods

To fully understand the role of diaspores we must sample them. The methodology influences what we sample, so it is worthwhile to examine these first.

The most commonly used means of sampling spores and other diaspores in the atmosphere is to place open

Petri dishes with a common bryophyte nutrient agar in the field at various heights and distances from a known source for a species. For shorter distances, one can use **glass slides** coated with glycerine. The spores usually cannot be identified by themselves, unless one has considerable experience and a good set of pictures and/or samples for verification. Hence, they must be germinated and the developing protonemata must be coaxed to develop and produce gametophores. Even then, one cannot be certain that the ensuing growth form is representative, since the light is artificial, may be too low or too high, certain growth factors available in its environment may be missing, and nutrients may be at inappropriate levels.

Other traps can include filters or air funnels in strategic positions that catch microbiota carried by drafts and other wind patterns. Each of these methods has its drawbacks, in addition to the problems of culturing and identification. Contamination is certain, density is low, and local micropatterns in air movements may be more influential in what they record in some cases than major pathways.

Levetin *et al.* (2000) compared the **Tauber trap** (Figure 2-Figure 3) with the **Burkard volumetric spore trap** (Figure 4-Figure 5), the latter a trap used in Antarctica (Lewis Smith 1991). The Burkard volumetric spore trap is used primarily for collecting airborne pollen, whereas the Tauber trap is used primarily to analyze deposition. They found a strong correlation between the pollen trapping recorded by the Tauber traps and the cumulative sums of average daily airborne spores/pollen from collections with the Burkard spore trap. Peck (1972) used the Tauber trap to sample pollen in turbulent flow water and found that under those conditions the collection efficiencies for individual taxa vary with both size and weight of the grains and velocity of flow. Smaller grains were trapped less efficiently than larger ones. As the water speed increased, grain characteristics had less effect, but the trapping efficiency decreased.

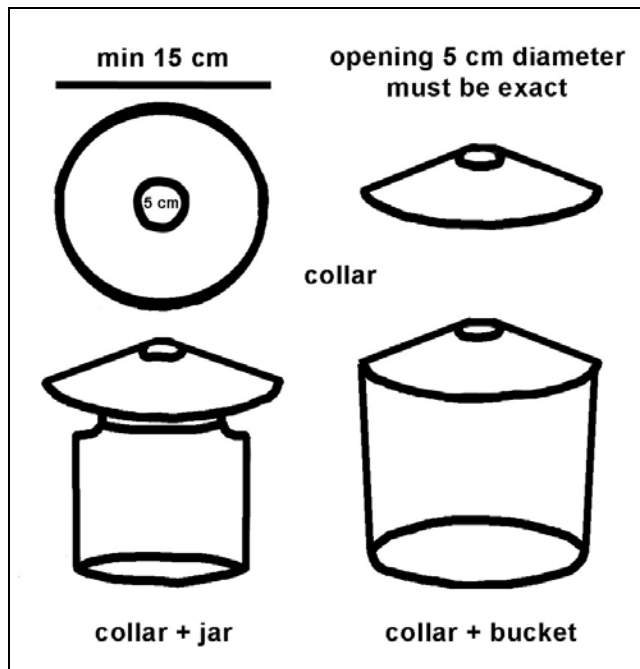


Figure 2. Tauber trap. Drawing based on Pardoe *et al.* 2010.

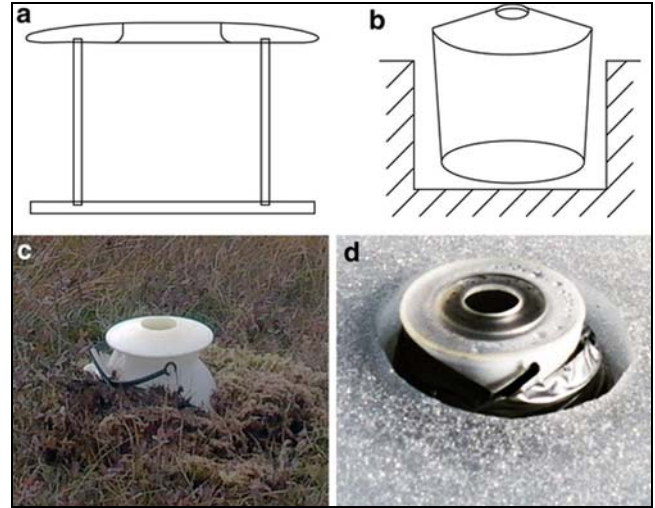


Figure 3. Tauber's original design (a & c) compared to the modification used with the Pollen Monitoring Programme (PMP) (b & d). Images from Pardoe *et al.* 2010, through Creative Commons.



Figure 4. Burkard volumetric spore trap. Photo by Burkard at <<http://www.burkard.co.uk/7dayst.htm>>, with permission.

More sophisticated samplers collect, filter, and concentrate the spores. One that has been used in bryophyte studies is the Rotorod sampler (Rotorod® Sampler 2009). This is a programmable instrument with a

timer that spins the head, bringing the pollen-collecting rods out by gravity. Its standard sampling is a 10% duty cycle, meaning that it samples for one minute out of every ten. A 5% duty cycle would collect for 30 seconds out of every ten minutes. Spores are collected on polystyrene rods pre-greased with silicone grease. To count the spores, the rod is placed in one of the deep grooves of a microscope stage adapter and a few drops of Calberla's stain applied. The rod is covered with a standard coverslip at the distal end of the rod and the spores are counted under a compound microscope at 400X. I am concerned that this rod is apparently intended to be used again and could easily have remnants of spores from a previous sampling, despite careful cleaning. A reticule can be used to aid in counting and to calibrate. The company has found that 400 spores are sufficient to get an accurate estimate of what is there.

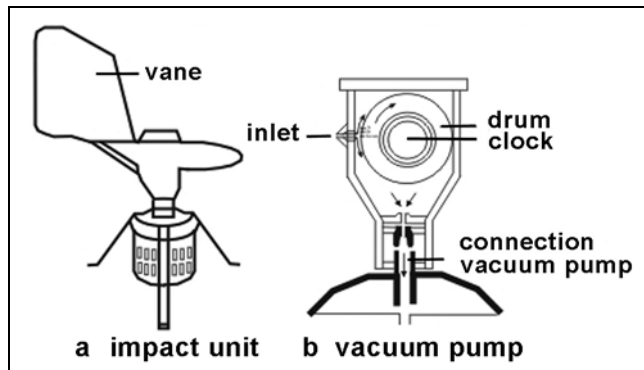


Figure 5. Burkard volumetric spore trap. Redrawn from Aerobiological Sampling, Universidad D Cordoba.

Nature provides her own traps that we can use, but these are varying pictures of time and not necessarily indicative of the present. In the Antarctic, snow provides an appropriate medium for analysis of deposition of diaspores (Lewis Smith 1991). And peatlands have been traditionally sampled for pollen as well as spores.

But not all evidence comes from trapping diaspores. Patterns of bryophyte distribution can help us to hypothesize the pathways and mechanisms. Lönnell (2011) summarizes indirect connections that can contribute to our understanding of dispersal:

1. genetic similarity between populations in different locations
2. successful colonization that can be connected through distribution patterns
3. diaspore longevity compared to species distribution
4. species composition with prevailing winds.

One problem with assessing the relative importance of asexual vs sexual reproduction is that we often misunderstand the mechanisms used by a species. Fritz (2009) demonstrated this for several pleurocarpous species. *Pseudoscleropodium purum* (Figure 6) and *Pleurozium schreberi* (Figure 7) are known for rarity of sporophytes, but Fritz found that genetic evidence of new gene combinations suggested that sexual reproduction followed by spore production was more common than suspected. This was further supported by finding frequent presence of both antheridia and archegonia.



Figure 6. *Pseudoscleropodium purum* with capsules in Bawsey Country Park, UK. Photo by Des Callaghan, with permission.



Figure 7. *Pleurozium schreberi* showing dying basal portion of stem that can result in the living portion becoming a separate plant, creating reproduction by cloning. Photo by Janice Glime.

Diaspore Banks or New Arrivals?

Leck and Simpson (1987) examined the spore bank in a Delaware River, USA, freshwater tidal wetland. Their samples came from rainwater, 0-2 cm, 4-6 cm, and 8-10 cm depth in high marsh, cattail, and shrub forest. These samples revealed 14 moss species and 2 liverwort species. The most common bryophyte was a species of *Bryum*. The 0-2 cm samples had more species and greater densities, but no cover. The sample spores required longer germination times in culture than what is typical for seed bank spores and may explain the lack of cover on the tidal surfaces.

In a forested floodplain in Ohio, USA, McFarland and Wistendhal (1976) found six species of mosses, with *Eurhynchium hians* (Figure 8) being dominant. In this case, they considered low light levels and occasional flooding to promote protonemal growth. Samples of soil with plants and fragments buried under 10 cm of alluvium had good regrowth and appear to be important to the establishment of terrestrial mosses on these flood plains.

Diaspores for colonizing an area can arrive from elsewhere or be exposed from propagules that have been buried and dormant. In areas experiencing recolonization,

propagule sources can arrive quickly from **diaspore banks**, those buried propagules that have survived for long periods until such time as they are once again returned to a position with sufficient light and moisture to grow. In this case, travelling the distance means travelling down to a depth where they can survive until they once again experience a favorable location. This may mean not travelling too far so that they never again surface; in other cases, deeper is safer.



Figure 8. *Eurhynchium hians* in Europe. Photo by Michael Lüth, with permission.

Heinken *et al.* (2004) found three recolonization mechanisms at work in pine forest gaps in Central Europe. These were 1) advance of shoots from the edge of the gaps through clonal growth; 2) dispersal of detached individual shoots and clumps; 3) regeneration of what appeared to be dead stems from a soil diaspore bank. Each of the regenerating species seemed to be best at one of the strategies. Disturbance temporarily increased diversity as colonists succeeded on newly available ground before the perennial stayers were able to completely occupy the gap.

Arrival can account for differences in species dominance. In a boreal forest, *Pleurozium schreberi* (Figure 7) didn't show any diaspore limitation (Lloret 1994). *Dicranum scoparium* (Figure 9) cover was not influenced by proximity of its neighbors, but it did increase its colonization when the species was introduced by planting. In these forest sites, *D. scoparium* seemed to depend on the diaspore bank for its establishment. *Hylocomium splendens* (Figure 180), on the other hand, did depend on the presence of neighbors.

Activation conditions usually mean reaching not only sufficient moisture, but being exposed to light. Continued metabolic activity without light is certain death, but most species seem to have mechanisms to prevent germination until light is available. For example, diaspore banks of the forest floor can be activated for germination by disturbance that brings propagules into sufficient light and available moisture (Korpelainen *et al.* 2011). Such diaspore banks may be the source of rapid colonizers after forest harvesting (Caners *et al.* 2009), mining of peatlands (Poschlod 1995), or other soil/substrate disturbances.



Figure 9. *Dicranum scoparium*. Photo by Janice Glime.

Even within the same habitat, the diaspore bank can differ based on the medium. In the bushland of western Australia, Biggs and Wittkuhn (2006) found 11 bryophytes in the soil and 13 in the litter. *Tayloria octoblepharum* var. *octoblepharum* (Figure 10) and *Rosulabryum campylotheceum* (Figure 11) only occurred in soil diaspore bank samples and *Lunularia cruciata* (Figure 12), *Fissidens serratus* (Figure 13), *Racopilum cuspidigerum* var. *convolutaceum* (Figure 14), and *Tortula antarctica* (Figure 15) only occurred in litter samples. *Bryum argenteum* (Figure 16) and *Rosulabryum billardieri* (Figure 17) were present in soil samples from all nine floristic types (including various types of woodlands, shrublands, heath, and mobile dunes); *Gymnostomum aeruginosum* (Figure 18) occurred in litter from all nine floristic types. As in other studies discussed herein, the diaspore bank housed some species that rarely occurred above ground, e.g. *Riccia* (Figure 97) and *Physcomitrium* (Figure 20). Among the familiar taxa from studies in other parts of the world were *Funaria hygrometrica* (Figure 164) and *Pohlia nutans* (Figure 36) in these Australian diaspore banks.

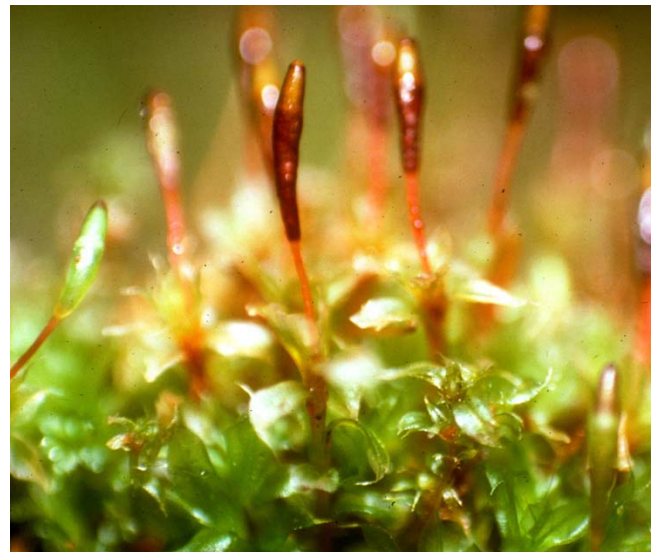


Figure 10. *Tayloria octoblepharum* with capsules. Photo by Janice Glime.



Figure 11. *Rosulabryum campylothecium*, a species common in soil diaspore banks but not in litter. Photo from British Bryological Society website, with permission.



Figure 12. *Lunularia cruciata* showing gemmae. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.



Figure 13. *Fissidens serratus* germinating bud. Photo by Tom Thekathyl, with permission.



Figure 14. *Racopilum cuspidigerum*. Photo by Jan-Peter Frahm, with permission.



Figure 15. *Tortula antarctica* with capsules, a species for which spores occur in the litter but not in the soil of Australian bushland. Photo by M. Fagg, Australian National Botanic Gardens <www.anbg.gov.au>, with online permission.



Figure 16. *Bryum argenteum* males. Photo by George Shepherd, through Creative Commons.



Figure 17. *Rosulabryum billardieri*. Photo by Tom Thekathyl, with permission.



Figure 18. *Gymnostomum aeruginosum*. Photo by John Game, through Creative Commons.

During (2001) considers that species such as *Micromitrium tenerum* (Figure 19) and *Physcomitrium sphaericum* (Figure 20) that require "episodically suitable habitats" persist in the diaspore bank as spores. In Mediterranean habitats where conditions permit winter annuals to persist, a sporebank is likewise an important source. On the other hand, in temperate forests and grasslands, long-lived shoots (especially pleurocarpous mosses) are rare in the diaspore bank even if numerous on the surface, whereas the short-lived species are typically over-represented in the diaspore bank, often as asexual propagules, awaiting small-scale disturbance.



Figure 19. *Micromitrium tenerum*, an ephemeral moss. Photo by Jan-Peter Frahm, with permission.



Figure 20. *Physcomitrium sphaericum* with protonemata, leaves, and capsules. Photo by Michael Lüth, with permission.

During (2001) considers that ruderal species often produce several types of propagules that are suitable for

different conditions. One such species is *Blasia pusilla* (Figure 21), which has stellate gemmae (Figure 22-Figure 23) that have two auricles with the nitrogen-fixing Cyanobacterium *Nostoc* (Figure 24) and large amylochloroplasts in the gemmae. Its second type of gemma is ellipsoid or ovoid (Figure 25) and produced in flask-shaped structures (Figure 21-Figure 26). They are filled with starch, proteins, and lipids but lack *Nostoc* (Duckett & Renzaglia 1993). The stellate gemmae are produced throughout the growing season, but do not survive the winter cold. The ellipsoid gemmae are not released until late summer or autumn and do survive winter, germinating in the spring. These latter gemmae are suitable for the diaspore bank, but their presence there does not seem to be documented (During 2001). It is likely that other taxa with multiple diaspore types likewise have a division of labor.



Figure 21. *Blasia pusilla* showing flask-shaped stalks with gemmae on top. Photo by Dick Haaksma, with permission.

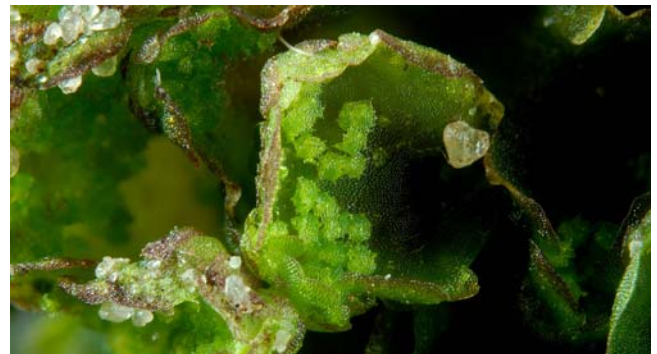


Figure 22. *Blasia pusilla* showing stellate gemmae. Photo by Dick Haaksma, with permission.



Figure 23. Stellate gemma of *Blasia pusilla* with *Nostoc* colonies. Photo by Dick Haaksma, with permission.



Figure 24. Thallus of *Blasia pusilla* with dark-colored *Nostoc* colonies. Photo by Walter Obermayer, with permission.

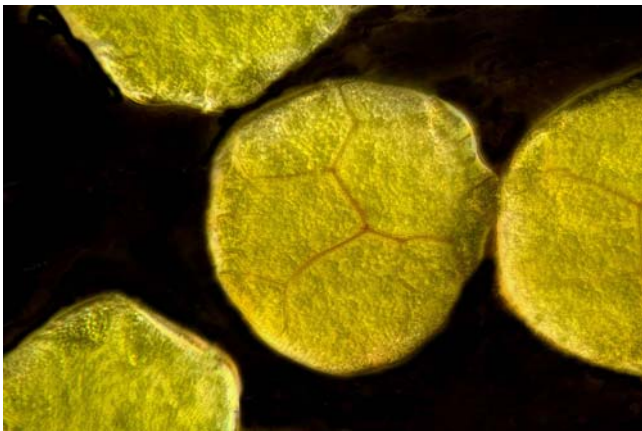


Figure 25. *Blasia pusilla* elliptical gemmae from the flask-shaped stalk. Photo by Dick Haaksma, with permission.



Figure 26. *Blasia pusilla* flask-shaped stalk with gemmae on top. Photo by Des Callaghan, with permission.

Species Differences

Not all diaspores enter the diaspore bank equally. Representation in diaspore banks is not necessarily a good

indication of what grows at the surface. During (1997) found that species that were short-lived above-ground were usually over-represented in the diaspore bank, but perennial species tended to be absent or rare. These diaspore bank species tend to have large spores, but many are only represented by vegetative diaspores.

Lönnell (2011) reviewed dispersal literature and concluded that diaspore banks have little representation by even dominant pleurocarpous mosses, whereas the short-lived species that one can easily miss in the flora are common in the diaspore banks. This may account for the observations of Vitt (2006), who summarized previous studies and concluded that diaspore banks usually lack good representation of the extant community. Instead, he found that the species dominating the current community are generally rare or absent in the diaspore bank; rather, spores present in the diaspore bank represent pioneer species that are not present in more mature stages. This latter statement supports the conclusion of Lönnell (2011) that the short-lived species are the most common. Lönnell also found that larger diaspores are better represented than smaller ones. This latter strategy is useful for species that must await an opening, then accomplish their life cycle quickly before the competition arrives. During *et al.* (1987) demonstrated that even in diverse habitats in Spain, this bias holds true. They found tubers, gemmae, leaf fragments, and viable cells on decaying stems in the diaspore banks. Despite the mix of bryophytes growing on the surface, the diaspore bank was dominated by species with a colonist life strategy. On the other hand, Poschlod (1995) concluded that for disturbed (mined) peatlands, recolonization is from the diaspore bank.

During and ter Horst (1983) found 37 species in the diaspore bank of a chalk grassland. Among these the **acrocarpous** (having archegonia terminal on upright stems; mostly growing vertically) colonists were likewise the most frequent, despite dominance of **pleurocarpous** (having archegonia on short side branches; mostly growing horizontally) mosses and perennial liverworts on the surface. During (1990) suggested that high species diversity in chalk grasslands might be maintained by intermediate disturbances that cause a high turnover of species originating from the diaspore bank.

During and Moyo (1999; During 2003) found that in a Zimbabwean savannah, fire did not seem to harm the diaspore bank. Following disturbance by burning, only *Exormotheca holstii* (Figure 27), 2 *Riccia* spp (Figure 97), 2 *Archidium* spp (Figure 109) and *Bruchia* (Figure 28) emerged from soil samples near the surface in the middle of the rainy season (During & Moyo 1999; During 2003). Nevertheless, in soil samples representing the diaspore bank 11 liverworts and hornworts and 21 moss species were present. As seen in a number of other studies, taxa often were absent in the surface flora and appeared only when the right disturbance conditions occurred (During 2007). During and Moyo (1999) found that some rare species and even some species previously unknown for that region were conserved in the diaspore bank (During & Moyo 1999; Zander & During 1999).

Some species always seem to be there when the landscape is scoured for a road cut or for making a ski trail. Such is the case for *Trematodon ambiguus* (Figure 29). In fact, this species had been considered to be extinct in

Belgium and the Netherlands, but following large-scale disturbance it reappeared, apparently from a long-lived spore bank in the soil (During *et al.* 2006). The spores are somewhat large (~30 μm), not especially numerous in the capsule (~14,000), and emerged from soil samples taken at 0-3 cm.

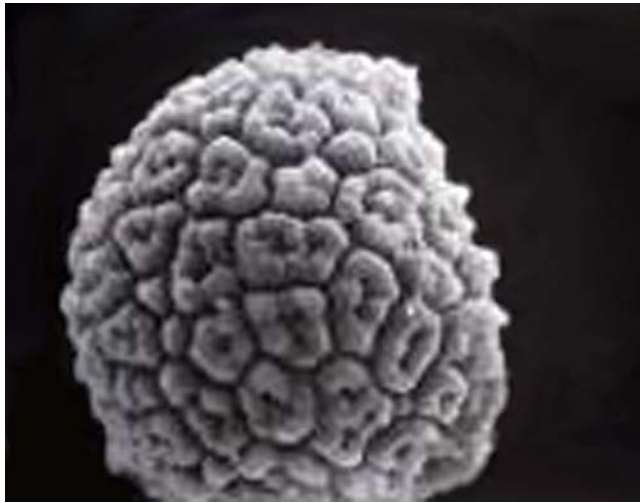


Figure 27. *Exormotheca holstii* spore, a propagule that can regenerate after fires in the Zimbabwe savannah. Photo by Laura Forrest, permission pending.



Figure 28. *Bruchia flexuosa*, a species that can emerge from the diaspore bank after fire. Photo by John Game, through Creative Commons.



Figure 29. *Trematodon ambiguus* capsules in an exposed soil bank along a new ski trail in Houghton, MI, USA. Photo by Janice Glime.

While not all bryophytes enter the diaspore bank equally, neither do they emerge equally. In a different road-cut study, Hassel and Söderström (1998) found that two species of *Pogonatum* behaved differently. *Pogonatum dentatum* (Figure 30) was most likely to occur on roads only 0-4 years old, whereas *P. urnigerum* (Figure 31) was more likely along roads more than 4 years old. At least for *P. dentatum*, frequency in the diaspore bank decreased with distance from parent colonies, suggesting that the diaspore bank is more important than diaspore rain.



Figure 30. *Pogonatum dentatum*, a species that appeared along new road cuts. Photo by Michael Lüth, with permission.



Figure 31. *Pogonatum urnigerum* with capsules and young male splash cups (unopened). This species appeared along road cuts more than 4 years old. Photo by Michael Lüth, with permission.

Some tuber-bearing mosses (Figure 35) seem to be especially dependent on diaspore banks. They may be very common in the diaspore bank, but absent on the surface until the soil is disturbed (During 1995). Where they do occur on the surface, maintenance of that population seems to depend on occasional recruitment from the diaspore bank. Nevertheless, they can still exhibit clonal behavior because the tubers are deposited near the parent on relatively long rhizoids.

Arable Fields

In three cultivated fields of Switzerland, Bisang (1996) found *Anisothecium staphylina* (Figure 32), *Dicranella schreberiana* (Figure 33), *Bryum rubens* (Figure 34-Figure 35), *Pottia* sp (Figure 118), and *Phascum* sp (Figure 61) as common members of the soil diaspore banks. As is typical, some species were present in the diaspore bank but not

present among the flora of that field. Species of diaspores in these agricultural habitats varied most between localities.



Figure 32. *Anisothecium staphylinia*, a species that appears after disturbance of cultivated fields in Switzerland. Photo by Michael Lüth, with permission.



Figure 33. *Dicranella schreberiana* with capsules, a species common in diaspore banks of arable fields. Photo by Michael Lüth, with permission.



Figure 34. *Bryum rubens* growth habit, a species common in arable fields in Switzerland. Photo by Michael Lüth, with permission.



Figure 35. Rhizoidal tubers on *Bryum rubens*. Photo by Jan-Peter Frahm, with permission.

Ponds and Lakes

One common bryophyte in the mud of ponds and lakes is *Physcomitrium sphaericum* (Figure 20). This species is not a regular member of the flora surrounding these water bodies because it requires conditions that are not present annually: exceptionally warm, dry summers (Furness & Hall 1981). In fact, the spores will germinate only in the range of 15-35°C. Its appearance under those suitable conditions is possible only because its spores remain viable in the mud for a long time.

Forests

The role of diaspore banks in various forested landscapes has been investigated through several studies. Caners *et al.* (2009) used mineral soil samples from mixed and coniferous stands of boreal mixed-wood forest in northern Alberta, Canada, to examine the role of these potential diaspore banks in reforestation after harvesting. Surprisingly perhaps, the composition of bryophyte species that were able to germinate related not to the forest types or harvesting intensity (measured by light regime), but to edaphic factors and, not surprisingly, to spatial proximity. Spatial proximity not only accounted for the species available, but also accounted for edaphic similarities. Nevertheless, light intensity had a significant influence on both the responses of individual species and on the species assemblages that arose.

In the boreal forest, Jonsson (1993) found 40 species, similar to the number found by During and ter Horst (1983) in chalk grasslands, of liverworts and mosses in the diaspore bank of an European *Picea abies* forest. The most abundant taxa were *Pohlia nutans* (Figure 36-Figure 37), *Sphagnum* spp. (Figure 47-Figure 52), and *Polytrichum commune* (Figure 88-Figure 89) / *Polytrichastrum longisetum* (Figure 38). In the boreal forest soil diaspore bank in southeastern Norway, Rydgren and Hestmark

(1997) found that *Plagiothecium laetum* agg. (Figure 39) and *Polytrichum* spp. (Figure 88-Figure 89) were the most frequent bryophytes germinating. Sean Robinson succeeded in growing new plants from a plant fragment of *Pohlia nutans* (Figure 37).



Figure 36. *Pohlia nutans* becoming established on sand. Photo by Des Callaghan, with permission.

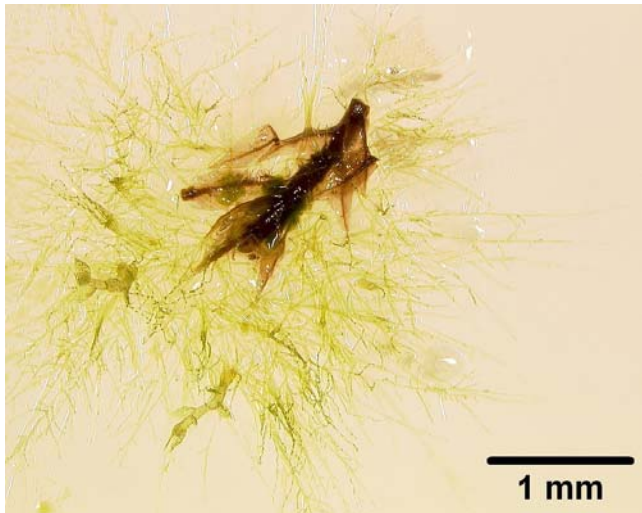


Figure 37. *Pohlia nutans* growth from fragments. Photo by Sean Robinson, with permission.



Figure 38. *Polytrichastrum longisetum* with capsules and mixed with *Campylopus* sp. Photo by David T. Holyoak, with permission.



Figure 39. *Plagiothecium laetum*. Photo courtesy of Betsy St. Pierre.

Forest gaps benefit from diaspore banks. Palisaar and Poschlod (2001) found that both forest and windthrow areas have a predominance of long-lived species, but the colonist strategist predominates in the diaspore bank, ready to take advantage of large, sunny gaps.

Tropical forest diaspore banks have rarely been studied, but it appears that their composition follows different patterns from those of other forests and periodically disturbed habitats. In lab cultures of diaspore banks from Brazil, bark (68) and decaying wood (55) species dominated, compared to soil species (22) (Maciel-Silva *et al.* 2012). Mosses were more numerous in both species and number of shoots than liverworts. Monoicous species were more common than dioicous species. Species that produced sporophytes and those producing gemmae were well represented in the diaspore banks. The biggest difference was that the diaspore banks represented the growing vegetation rather well.

When culturing samples from the diaspore bank of three Malaysian mountain rainforests, Bisang *et al.* (2003) found germination of more liverworts than mosses, especially from the lower altitudes, contrasting with the results of Maciel-Silva *et al.* (2012). These liverworts [*Cincinnulus* (as *Calypogeia*) *argutus* (Figure 40), *Mnioloma* (as *Calypogeia*) *fuscum*, *Lepidozia wallichiana* (Figure 41), and *Zoopsis liukuensis* (Figure 42)], were, as in the study of Maciel-Silva *et al.*, common taxa growing in the area. Stem fragments that had lost their chlorophyll seemed to be the diaspores that gave rise to *Isopterygium* sp. (see Figure 43) and cf. *Ectropothecium* sp. (Figure 44), but for other taxa they were unable to identify the type of diaspore.



Figure 40. *Cincinnulus argutus*, a species in tropical diaspore banks. Photo by Des Callaghan, with permission.

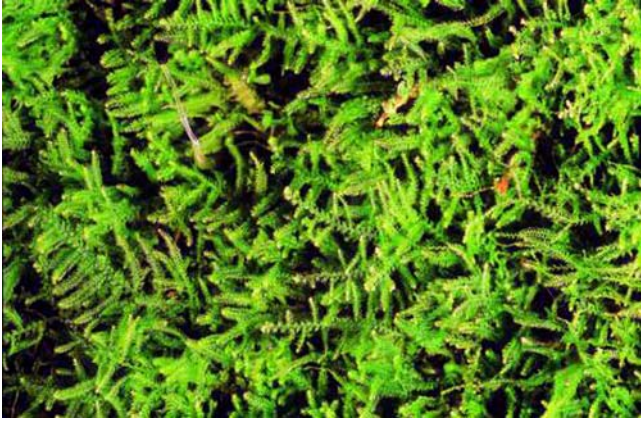


Figure 41. *Lepidozia wallichiana*, a species in tropical diaspore banks. Photo by Jia-Dong Yang, through Creative Commons.



Figure 44. *Ectropothecium perrotii*, a species in tropical diaspore banks. Photo by Jan-Peter Frahm, with permission.



Figure 42. *Zoopsis liukuensis*, a species in tropical diaspore banks. Photo by Rui-Liang Zhu, with permission.



Figure 43. *Pseudotaxiphyllum elegans* with gemmae, a species in tropical diaspore banks. Photo by Jan-Peter Frahm, with permission.

Peatlands

In peatlands, recolonization is derived from diaspore banks and adjoining similar habitat. Sundberg and Rydin (2000) showed experimentally that 15-35% of *Sphagnum* spores could survive for 13 years when stored in humid conditions such as would be present in a peatland diaspore bank.

Campbell *et al.* (2003) found that in a regenerating Quebec, Canada, peatland, *Polytrichum strictum* (Figure 45) was widespread and its colonization showed no significant trends with distance from a living source. *Pleurozium schreberi* (Figure 46), *Sphagnum capillifolium* (Figure 47), and *Sphagnum fuscum* (Figure 48), on the other hand, only became frequent further from edges (> 20 m), suggesting that the right habitat conditions were absent at the edges. They explained the strong presence of *Polytrichum strictum* by the long fall times from capsule to substrate, coupled with its very small spores, facilitating its travel despite its low release height. Nevertheless, the diaphragm forces the spores out the sides, a position not conducive to aerial transport.



Figure 45. *Polytrichum strictum* with capsules in Europe, a species whose regenerating capacity does not seem to relate to distance from source. Photo by Michael Lüth, with permission.



Figure 46. *Pleurozium schreberi* in Michigan, USA. Photo by Janice Glime.



Figure 49. *Sphagnum angustifolium*, a species not detected in the diaspore rain of a regenerating peatland, but nevertheless present as a regenerant. Photo by Michael Lüth, with permission.



Figure 47. *Sphagnum capillifolium*, a species that did not regenerate close to the edges of the peatland. Photo by David Holyoak, with permission.



Figure 50. *Sphagnum papillosum*, regenerating species absent from diaspore rain. Photo by Michael Lüth, with permission.



Figure 48. *Sphagnum fuscum* in Alaska, USA, a species that did not regenerate close to the edges of the peatland. Photo courtesy of Andres Baron Lopez.

On the other hand, *Sphagnum angustifolium* (Figure 49), *S. papillosum* (Figure 50), *S. cuspidatum* (Figure 51), *S. subsecundum* (Figure 52), *Pleurozium schreberi* (Figure 46), *Leucobryum* sp. (Figure 53), and *Chiloscyphus profundus* (= *Lophocolea heterophylla*) (Figure 54) were present in the vegetation and absent in the measured diaspore rain of the regenerating peatland (Campbell *et al.* 2003).



Figure 51. *Sphagnum cuspidatum*, regenerating species absent from diaspore rain. Photo by Michael Lüth, with permission.



Figure 52. *Sphagnum subsecundum*, a regenerating species absent from the diaspore rain. Photo by Michael Lüth, with permission.



Figure 53. *Leucobryum glaucum* with capsules. Note the broken leaves lying on the surface of the cushion. Photo by Janice Glime.



Figure 54. *Chiloscyphus profundus*, a regenerating species absent from the diaspore rain of a peatland in Canada. Photo by Michael Lüth, with permission.

Poschlod (1995) conducted extensive studies comparing milled peatlands to natural raised bogs in the Bavarian foothills of the Alps. He found for those peatlands that recolonization apparently came entirely from diaspore banks, especially for *Sphagnum* species. That

genus was entirely absent in the spore rain sampled. In particular, *Sphagnum magellanicum* (Figure 55), *S. capillifolium* (Figure 47), and *Polytrichum strictum* (Figure 45) occurred in the diaspore rain in at least one of the six sites studied.



Figure 55. *Sphagnum magellanicum* in Europe, a species that regenerates from diaspore banks. Photo by Michael Lüth, with permission.

Among the bryophytes in these peatland diaspore banks, Poschlod (1995) found six species of liverwort fragments. Of these, five of these are species that develop tubers. Furthermore, *Cephalozia connivens* (Figure 56) and *Kurzia pauciflora* (Figure 57) have subterranean shoot axes and *Calypogeia* (Figure 58) species have a shoot axis near the surface. Duckett and Clymo (1988) likewise found liverwort shoot axes in bogs in Great Britain and estimated that regeneration came from peat layers that were 25-60 years old. Based on studies by Clymo and MacKay (1987), they ruled out downwash into deeper layers.



Figure 56. *Cephalozia connivens* in Europe, a species that can persist in diaspore banks by its subterranean shoots. Photo by Michael Lüth, with permission.



Figure 57. *Kurzia pauciflora* in Europe, a species that can persist in diaspore banks by its subterranean shoots. Photo by Michael Lüth, with permission.



Figure 58. *Calypogeia fissa*, a species that can persist in diaspore banks by its subterranean shoots. Photo by Hermann Schachner, through Wikimedia Commons.

Poschlod (1995) found all the *Sphagnum* species typical of raised bogs in the diaspore banks. Brown stems and branches of *S. capillifolium* (Figure 47) and *S. cuspidatum* (Figure 51) were able to regenerate from depths down to 15 cm. Peatland diaspore banks can be deep, with viable *Sphagnum* spores occurring as deep as 30 cm (Poschlod 1995). Poschlod (pers comm. 28 March 2013) concluded from this that the spores could survive more than two centuries!

Delayed Germination – Dormancy

Propagules may survive diaspore banks through dormancy (Hock *et al.* 2004). In two open grasslands in Hungary, gemmae of a species in the *Bryum atrovirens* complex (Figure 59) and *Weissia controversa* (Figure 60) exhibited dormancy. Likewise, dormancy seemed to be present in the spores of *Tortula acaulon* (= *Phascum cuspidatum*) (Figure 61). Hock *et al.* suggested that dormancy may be relatively common for diaspores of species living in habitats with short-term periods of unfavorable growing conditions.

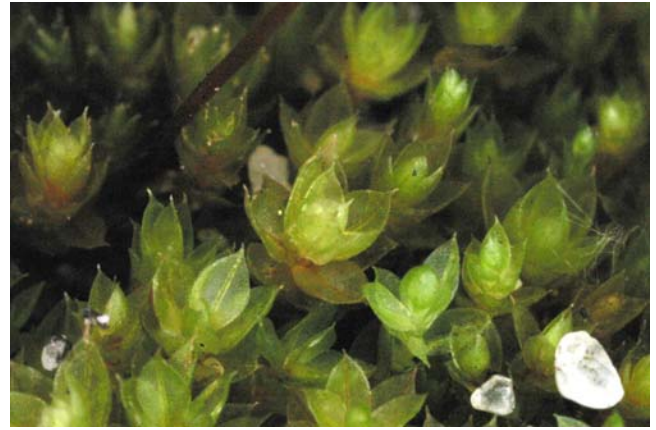


Figure 59. *Bryum atrovirens* aggregate. Photo by Jan-Peter Frahm, with permission.



Figure 60. *Weissia controversa* var. *controversa* with capsules. Photo by David Holyoak, with permission.



Figure 61. *Tortula acaulon* (= *Phascum cuspidatum*) with capsules. Photo by David Holyoak, with permission.

It is interesting that initially the highest number of species in the boreal forest diaspore bank arose from the mineral soil (9.9 per sample), but after four years the reverse was true (Jonsson 1993), with more arising from the humus, suggesting that some species have a delay mechanism that does not permit them to germinate right away. Watson (1981) suggested that *Polytrichum* species had the option of chemical inhibition to facilitate dormancy. Such delay mechanisms are known from flowering plants and include such factors as immature embryos (not applicable to bryophytes), chemical inhibitors

that must be washed away or removed by digestive enzymes of an animal (not yet shown for bryophytes but possible), or the need for hormones or vitamins from a fungal or bacterial partner [known for development of the gametophore in *Pylaisiella selwynii* (Figure 62) and several other moss species (Spiess 1977, 1979; Spiess & Lippincott 1978; Spiess *et al.* 1971, 1972, 1973, 1976, 1981a, b, 1982, 1984a, b, c, d, 1986, 1990)]. I have cultured *Fontinalis squamosa* (Figure 63) that produced protonemal gametophore buds in the presence of contamination while the cultures that remained sterile produced no buds. What other examples of bryophytes are out there in nature where a living partner is needed to provide some growth factor necessary for development to continue – or even start?

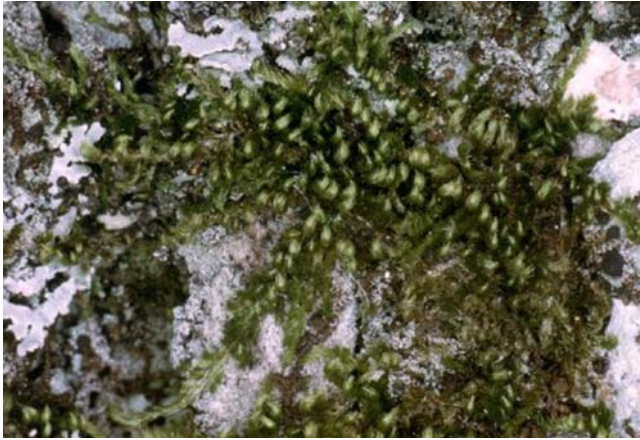


Figure 62. *Pylaisiella selwynii* on bark, a species that requires a bacterial partner to complete its development. Photo by Jan-Peter Frahm, with permission.



Figure 63. *Fontinalis squamosa* in Europe, a species that may require a bacterial partner to develop protonemal buds. Photo by Michael Lüth, with permission.

Other factors relating to delay of germination may be habitat condition or suitable weather. For example, in *Sphagnum* (Figure 47-Figure 52), dormancy may be conditional, depending on weather (Sundberg & Rydin 2000).

This leads us to ask what conditions are needed to break dormancy. Obviously, water is needed, and for continued success, light is needed. But water may be insufficient for continued development, so the spore needs a way to prevent germination when conditions are not likely to remain suitable. Mogenson (1981) suggested that spore surface sculpturing may serve to prevent small quantities of water from activating the spore by creating

surface tension that prevents the water from penetrating the spore. However, this hypothesis seems not to have been tested.

Blasia pusilla (Figure 22-Figure 26) is one liverwort whose gemmae do not germinate right away when brought to the surface from a diaspore bank (During 2001). Gemmae of *B. pusilla* do not germinate until the spring after their production (Duckett & Renzaglia 1993), a phenomenon well known for seeds. This delay could be related to its storage of food reserves as protein, which is slower to metabolize than the starch or oils of other spores (Crum 2001). It seems likely to me that there are other bryophytes that have this delayed germination mechanism in spores or other propagules, especially in the **Anthocerotophyta** with their protein food reserves (Crum 2001). The leafy liverwort *Lophozia ventricosa* var. *silvicola* (Figure 64) changes its dormancy based on the time of production, with those gemmae produced in the spring germinating readily, but those produced later seem to lose germinability with time of production (Laaka-Lindberg 1999). A similar seasonal relationship is known for the forest floor tracheophyte *Melampyrum lineare*. If a propagule begins to convert its food reserves, loss of water could stop the process and prevent germination. This could only happen a few times before the reserves are used up, and a small propagule would lose its reserves sooner than a large one.



Figure 64. *Lophozia ventricosa*. Photo by Hermann Schachner, through Creative Commons.

Asexual propagules likewise display dormancy. We have witnessed the effect of parents on inhibiting development of vegetative propagules, *e.g.* the absence of germination of *Marchantia polymorpha* gemmae (Figure 65) while they remain on the parent. There seem to be few species where either spores or vegetative propagules can germinate while still in contact with the parent, and many species, for example *Funaria hygrometrica* (Figure 164), are unable to germinate near their parents due to chemical inhibitors leached from the parent. Could there be biochemicals in the environment that must leach out before germination occurs in some species?

Even freshly produced spores may have dormancy (**innate dormancy**), as in *Archidium alternifolium* (Figure 66). This dormancy is broken slowly and the mechanisms for breaking it are unknown (Miles & Longton 1992). Germination was less than 65% and increased as the spores aged, up to 4 years. This delay suggests to me that there

may be a chemical inhibitor that is removed by leaching. In *Sphaerocarpos texanus* (Figure 67), spores are dormant when released, but dormancy is broken by fluctuating temperatures, typically 35/20°C and may even have dormancy/non-dormancy cycles resulting from temperature fluctuations (McLetchie 1999).

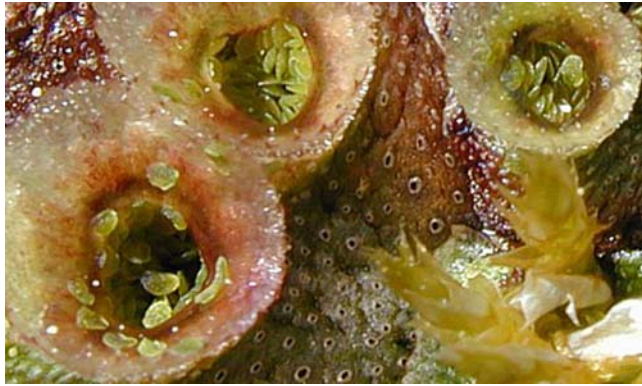


Figure 65. *Marchantia polymorpha* with gemmae. Photo by Michael Lüth, with permission.



Figure 66. *Archidium alternifolium*. Photo by Michael Lüth, with permission.



Figure 67. *Sphaerocarpos texanus* on disturbed soil. Photo by Adolf Ceska, with permission.

Dormancy relationships seem to be complex, making them difficult to predict. Kobayashi and Yamamura (2000) found that inbreeding caused an increase in dormancy, perhaps through complementation. But the spores have only one set of chromosomes, so this logic seems to fail. And under some conditions inbreeding leads to decreased dormancy – a combination of genes where dormancy is poor to start with? We also know examples where longevity of female spores is longer than that of male spores [McLetchie 1992 for *Sphaerocarpos texanus* (Figure 67)]. How does dormancy affect longevity?

The seed bank houses a set of seeds that represent a non-random set of genotypes. That is, at the seed bank level, there is selection. There is evidence that there are correlations among suites of characters such as temperature of response and seed longevity. Such relationships need to be explored for bryophytes. Furthermore, risk of predation by animals and attack by fungi are strong selection factors for seeds, but these likewise have received inadequate attention for bryophytes.

Does Depth Matter?

Bisang (1996) compared germination of diaspores from above and below 25 cm for diaspores that were disturbed by regular ploughing to a depth of about 10-25 cm. In general, protonemata of mosses were less vigorous in soil samples from below 25 cm. Furthermore, *Eurhynchium hians* (Figure 8) and *Riccia* sp. (Figure 97) were present only to a depth of 15 cm.

Benefits of Diaspore Banks

Diaspore banks that have a store of recent species are likely to provide the soil/substrate characteristics required for the successful re-establishment from diaspore growth, once they are in a position to obtain sufficient light and moisture. On the other hand, light conditions may differ from those when the diaspores were deposited, and the species represented are often different from those on the surface (During & ter Horst 1983; During 1997). Furthermore, the species richness of the bryophytes may be influenced by the species composition of tracheophytes that has developed while the diaspores lay dormant (Aude & Ejrnæs 2005). For the short-lived shuttle species of agricultural landscapes, even the soil characteristics may have changed due to agricultural practices of fertilizing, a condition that can be detrimental to many bryophytes adapted to low nutrient conditions.

Tradeoffs

Diaspores, like any other novel solution, have their tradeoffs, although our understanding of these is very limited. During (2001) suggests that the lack of perennial bryophytes in the diaspore bank represents a tradeoff between adult longevity and diaspore longevity. Spore size is another potential tradeoff. Species with small spores such as *Funaria hygrometrica* (Figure 164) tend to have short viabilities in the soil (During 1987). During (2001) suggests that a similar tradeoff between dispersability and soil longevity could account for the scarcity of such weedy species as *Marchantia polymorpha* (Figure 1), *Bryum argenteum* (Figure 16), *B. bicolor* (Figure 68), and *Ceratodon purpureus* (Figure 69) in soil diaspore banks.

Nevertheless, Biggs and Wittkuhn (2006) found *B. argenteum* in the soil diaspore banks in all nine habitats in their study in western Australia. Could it be that this is a different microspecies?



Figure 68. *Bryum bicolor* with capsules, a species with good dispersability and poor diaspore longevity. Photo by Jonathan Sleath, with permission.



Figure 69. *Ceratodon purpureus* in southern Europe, a species with good dispersability and poor diaspore longevity. Photo by Michael Lüth, with permission.

Rather than small spores and good dispersal, During (2001) finds that the overall trend in diaspore banks is just the opposite. Those species that persist in the soil diaspore bank tend to have large spores (Jonsson 1993). This is a reasonable expectation because it would make it possible for these species to grow rapidly when they do germinate, taking advantage of the absence of competition from tracheophytes. Furthermore, many of these species have cleistocarpous capsules and short setae, making dispersal to any distance an unlikely event.

This presence of large spores in the diaspore bank is in contrast to that of seeds, where small seeds predominate. During (2001) suggests that seed predation on larger seeds and ease of dispersability of small spores may account for the difference in relationships. Furthermore, asexual diaspores are much more common among bryophytes.

Spores vs Vegetative Dispersal

All bryophytes require dispersal in some form to continue the species as its current habitat changes or disappears. Spores may be especially important for colonizing epiphytic habitats and other vertical habitats

such as walls and cliffs, as well as being the primary source of propagules for forest clearings. Grime and coworkers (1990) contend that sporebanks are important in exploiting disturbed habitats, but even these sporebanks depend on aerial dispersal as well as local dispersal. These recolonization and new colonization events by spores are possible only because of the ease of dispersal of at least some of the spores.

Both spores and asexual diaspores provide the means by which bryophytes can reach new locations or spread in local ones. At some point, specialized asexual reproduction arose in photosynthetic organisms. Algae can make extensive use of fragmentation, and some algae have asexual spores. But bryophytes have developed specialized structures for their reproduction and never produce asexual spores, *i.e.*, they produce only meiospores.

We must ask then, what are the advantages of sexual vs asexual propagules, and under what circumstances? Newton and Mishler (1994) summarized our knowledge and pointed out that spores have a prerequisite of fertilization, and this process requires water. But spores usually disperse farther than vegetative propagules and germinate best in previously uncolonized substrates. Vegetative structures, on the other hand, can be produced even under stressful conditions, disperse well locally, and are more successful in germinating among existing colonies.

During (pers. comm. 5 January 2005), however, points out that in some cases, the role of spores in dispersal, particularly large spores, is very similar to that of asexual propagules, having short-range dispersal with greater chance of germination and establishment in a somewhat wider range of habitats. And if the species is **monoicous** (both sexes on same plant), it is likely that the spores resulted from selfing and thus have similar genetic makeup to that of any asexual diaspore that might be produced in the same species. Hence, there seems to be a trade-off in these species with large spores. There appears to be little advantage for them also to produce asexual structures for reproduction. This is especially true for annual shuttle species – these species may simply not have enough time to produce both, since many bryophytes typically do not have enough energy to produce sexual spores and vegetative diaspores at the same time, although they may ultimately be present at the same time.

Fritz (2009) tested the relative importance of asexual vs sexual reproduction in several species [*Pseudoscleropodium purum* (Figure 6), *Pleurozium schreberi* (Figure 7), and *Rhytidiadelphus squarrosus* (Figure 70)] where sporophytes are considered to be rare. First, he found that sporophytes were apparently not so rare, using molecular data to demonstrate that the level of genetic diversity was that to be expected from spore dispersal. In these small populations, the genetic structure showed positive correlations between genetic diversity of a population and sporophyte occurrence. It appears that there may be an energy tradeoff at work here, because Fritz found that in these three species, clonal plants were present primarily in small patches up to 6 m² and were restricted to populations where both antheridia and archegonia, as well as sporophytes, were absent, or where only one sex of gametangia was present. This would be a good contingency strategy – that of a **bet hedger**.



Figure 70. *Rhytidiadelphus squarrosus*. Photo by David Holyoak, with permission.

Pohjamo *et al.* (2006) compared spores and gemmae in the leafy liverwort *Anastrophyllum hellerianum* (Figure 71), where they are of equal size. Unlike the suggestion of During (pers. comm. 5 January 2005) that their dispersal distances would be equal, Pohjamo *et al.* found that dispersal distances differed, with gemmae travelling farther. Between 17.5 and 43.1% of the spores released and 0.64 and 4.8% of the gemmae available were deposited within 10 m of the central colonies. Rain had no effect on either dispersal pattern, but more gemmae were released on rainy days. This leaves us to wonder why gemmae travel farther. Perhaps their non-spherical shape causes them to be caught by the wind more easily, or to attach to animals more easily.

A number of species rarely produce capsules. If they likewise do not have any specialized reproductive structures, this presents a dispersal problem. But researchers continue to discover asexual means that were previously unknown or rarely described in floras. For example, despite the obvious presence of propagula in several species of *Aulacomnium*, these are seldom mentioned for *A. heterostichum* (Figure 72), but can be quite abundant in some populations (Imura *et al.* 1991; Figure 72). Such was the case for *Mnium stellare* (Figure 73), a species that rarely produces capsules in Europe. However, in 2012, Hugonnot and Celle discovered that it reproduces by leaf **fragmentation**. This is not just random fragmentation, but rather the result of both splitting (**schizogeny**) and breaking (**lysogeny**). In **lysogeny**, there is partial cell disintegration that facilitates the fragmentation. They suggested that **schizogeny** was probably the result of hydration of the middle lamella. In *Mnium stellare* the fragility of the leaves seems to be greater when the leaves are hydrated, rather than when they are dry. Hugonnot and Celle verified these fragments as legitimate dispersal units by showing that they readily germinated on wet peat. Other species are already known for their leaf fragmentation abilities, *e.g.* *Dicranum viride* (Figure 74), *D. fragilifolium* (Figure 75), *Tortella fragilis* (Figure 76).



Figure 71. *Anastrophyllum hellerianum* gemmae that are the same size as spores in this species. Photo by Des Callaghan, with permission.

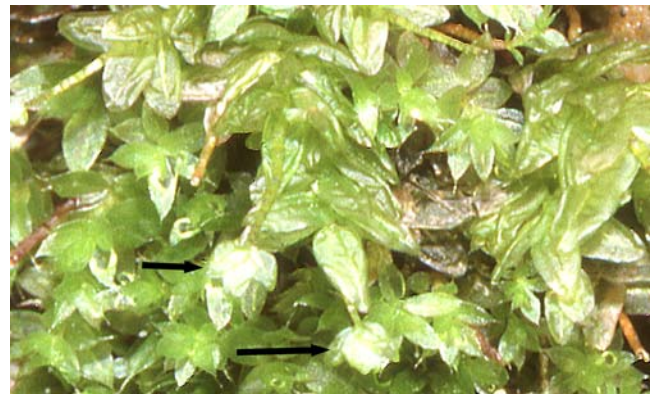


Figure 72. *Aulacomnium heterostichum* with propagules, indicated by the arrows. Note also the yellowish branch tips where these specialized leaves have been shed. Photo by Janice Glime.



Figure 73. *Mnium stellare* from the Khibiny Mountains, Apatity, Murmansk. Note the broken leaves at the arrows. Photo by Michael Lüth, with permission.



Figure 74. *Dicranum viride* showing broken leaves. Photo by Janice Glime.



Figure 75. *Dicranum fragilifolium* with broken leaf tips. Photo by Janice Glime.



Figure 76. *Tortella fragilis* with broken leaf tips. Photo by Michael Lüth, with permission.

Wang *et al.* (2012) used inter-sample sequence repeat markers and DNA sequences to investigate sexual vs asexual strategies in *Hypnum plumaeforme* (Figure 77) and *Pogonatum inflexum* (Figure 78). *Hypnum plumaeforme* reproduces primarily vegetatively. For this

species, the genetic diversity among island populations was significantly greater than that among lakeside populations where the habitat became available and isolated 50 years earlier, suggesting greater isolation among the island populations. *Pogonatum inflexum*, on the other hand, is frequently fertile, spreading primarily by spores. In this species there was no difference in genetic diversity between island and lakeside populations. Wang *et al.* (2012) considered this to be evidence that fragmentation of landscapes could increase genetic differentiation in species that have limited dispersal abilities, resulting in greater spatial differences in genetic structure.



Figure 77. *Hypnum plumaeforme* on bark, a species that reproduces primarily vegetatively. Photo by Janice Glime.



Figure 78. *Pogonatum inflexum*, a species that reproduces primarily by spores. Photo from the University of Hiroshima Digital Museum, with permission.

Understanding dispersal of bryophytes is complicated by their ability to disperse by more than one means. Furthermore, some species are not known to produce spores and others don't produce spores in some locations where only one gender is present. As an example, Bremer and Ott (1990) reported that nearly 40% of mosses in the Netherlands never or rarely produce spores. Nevertheless, the first bryophytes to colonize forests there are those that produce spores frequently, with those rarely producing spores [*Orthodicranum montanum* (Figure 79), *Rhytidiadelphus squarrosus* (=R. *loreus*; Figure 80), *Thuidium tamariscinum* (Figure 81)] arriving 20 years later. In these forests, experiments suggest establishment from spores is very rare for perennial stayers. It is only in older forests that one can find species with large spores.



Figure 79. *Orthodicranum montanum* showing dislodged bulbil (arrow). This species can form entire colonies of bulbils or form larger gametophyte stems accompanied by these bulbils. Photo by Janice Glime.



Figure 80. *Rhytidiadelphus squarrosus* (= *R. loreus*) with capsules. Photo by David T. Holyoak, with permission.



Figure 81. *Thuidium tamariscinum*, a moss that seldom produces capsules. Photo by Brian Eversham, with permission.

It is widely accepted that bryophyte spores are important for long distance dispersal to colonize newly available habitats (Newton & Mishler 1994). The time required, however, may be centuries or even millennia. Longton (1997, 2006) sums up the differences as one of spores being able to establish new populations more easily and asexual propagules being of major importance in colony expansion and maintenance.

Differences in Success

One question we might ask is why do some (actually many) bryophytes maintain both sexual and asexual reproductive propagules? Bengtsson and Ceplitis (2000) contend that for such a system to evolve and be maintained, the relative fitnesses of the sexual and asexual propagules must vary over the years. This would permit the most fit system to operate under the environmental conditions of that year. These conditions might be weather conditions, but they can also relate to competition, availability of bare soil, disturbance, herbivory, and other environmental factors. In this context, we might ask what hormonal changes occur in response to herbivory, or how does nutrient depletion affect asexual vs sexual reproduction? And if it is dry, will that stimulate asexual instead of sexual reproduction?

Frahm (2009) claims that there is no difference in effectiveness between sexual and vegetative propagation. He contends that the small size and weight of both spores and vegetative propagules would lead one to believe that both can be dispersed easily, thus supporting wide ranges for the species. Some species do have wide distribution, whereas others have very narrow ranges. And both of these categories include strictly vegetative reproducers and sexual (spore) reproducers. This disparity of ranges does not seem to relate to the abundance of propagules produced, with some species with high production of propagules demonstrating limited distribution and some sterile species having wide distribution (Frahm 2009).

But Callaghan and Ashton (2008) have arrived at a different conclusion for bryophytes in the British Isles. They found that among the 430 taxa there, range-size of both mosses and liverworts is significantly positively correlated with sporophyte production. But in seeming contradiction to this relationship, they found that **monoicous** (having both sexes on the same plant) moss species were rarer than **dioicous** (having the two sexes on different plants) species, suggesting that this rarity of monoicous taxa may be due to less fitness arising from self-fertilization.

Data on *Octoblepharum albidum* (Figure 82-Figure 83) demonstrate a different benefit than is typically attributed to gemmae. Their protonemata from gemmae grow faster than those from spores, most likely making their establishment more successful. On the other hand the spores produce more gametophytes. That is, one gemma produces one plant, but one spore produces many plants arising from multiple buds on a single protonema, at least for mosses.

It is not unusual for bryophytes to have more than one vegetative means of propagation. For example, *Rhytidium rugosum* (Figure 84-Figure 85) has three types of vegetative propagation: ramets (vegetative branches that separate by decay and disintegration when they are older; Figure 84); brood branches; and caducous branches (branches that easily break off as dispersal units; Figure 85). Pfeiffer *et al.* (2006) used AFLP fingerprinting to identify three clones from two plots, each having 2-15 samples with identical fingerprints. Presence of one clone in two plots indicates dispersal by vegetative diaspores. The close relationships between plots suggest that these plots were created through cloning, not spore dispersal.



Figure 82. *Octoblepharum albidum* with both capsules and gemmae (arrow). Photo by Li Zhang, with permission.



Figure 83. *Octoblepharum albidum* leaf with gemmae. Photo by Li Zhang, with permission.



Figure 84. *Rhytidium rugosum* showing dark bases of the ramet that will eventually decay and separate this piece (ramet) into a new plant. Photo by Michael Lüth, with permission.



Figure 85. *Rhytidium rugosum* demonstrating a dry branch that can easily be broken off (caducous) by a frisky squirrel. Photo by Michael Lüth, with permission.

Molecular data for *Pseudoscleropodium purum* (Figure 6) and *Pleurozium schreberi* (Figure 7) showed clonal reproduction [as in *Rhytidium rugosum* (Figure 84-Figure 85)] was an important part of their population dynamics (Fritz 2009). Fritz (2009) furthermore found possibilities for vegetative reproduction that had not yet been documented, including cloning, brood branches/branchlets, caducous shoot apices, and brood leaves (only in *P. schreberi*).

Löbel *et al.* (2009) compared mating systems and concluded that larger asexual diaspores enjoyed higher establishment rates at the cost of shorter dispersal distances, whereas the small sexual spores sacrificed establishment rate to achieve greater dispersal distances, a concept supported by the *Rhytidium rugosum* (Figure 84-Figure 85) study (Pfeiffer *et al.* 2006). This is an interesting contrast to that of Pohjamo *et al.* (2006) for the leafy liverwort *Anastrophyllum hellerianum* (Figure 71) where the vegetative gemmae travelled farther.

Limits to Success

These inconsistencies based on propagule size and abundance lead us to the conclusion that the propagules of different species have different abilities to arrive and colonize in new locations, using attributes independent of size. As Frahm (2009) points out, it suggests that the germinating propagule is limited by narrow ecological niches, age of taxon, local extinction, or historical events such as ice ages. Caners *et al.* (2009) also found that microhabitat conditions determine the success of species once they arrive or get exposed from soil banks. **Edaphic** (soil) factors are especially important, as well as habitable space. Although successful species composition did not relate to forest type or harvesting intensity, Caners and coworkers found that light intensity had a significant influence on the success of individual species and thus has important management implications in reforestation. To further their assertion of the importance of soil, we might consider the conclusions of Bischler and Jovet-Ast (1981) that in the **Marchantiales** (Figure 1) morphological characters may not be important to survival and dispersal, but rather their adaptations are primarily "linked to biochemical and biophysical properties of the cell content."

With respect to soil characters, I must caution about an area of research that has received little attention. In a new location, differences in soil chemistry could cause morphological differences that could cause even an astute systematist to assume a different species. This can of course be sorted out by DNA fingerprinting, but there is little experimental evidence to address this question. A few studies have, however, demonstrated the plasticity of species under different environmental conditions. For example, Zastrow (1934) cultured a variety of species and showed that responses to water culture include loss of central strand, papillae, alar cells, and leaf border, as well as showing reduction in costa and chlorophyll. Alkaline conditions caused stem elongation between nodes compared to that in neutral and acid conditions. Buryová and Shaw (2005) cultured six populations of *Philonotis fontana* (Figure 86-Figure 87) under two light and two water regimes and observed that both light and water affected growth, but cell dimensions seemed unaffected. Responses differed not only according to treatment, but also showed genetic differences in their responses. But others have shown changes in the number of cell layers in the stem of *Fontinalis* (Figure 63) species (Sée & Glime 1984). Such plasticity makes tracking species dispersal pathways more difficult and our understanding is likely to remain under constant revision for some time to come as molecular data refute our earlier hypotheses.



Figure 86. *Philonotis fontana* in a wet habitat where it can become submerged. Leaves produced in these submerged conditions can be smaller and more widely spaced than those grown aerically. Photo by Michael Lüth, with permission.



Figure 87. *Philonotis fontana* showing brood bodies at the tip of the stem. Photo by Janice Glime.

In recent years, genetic/molecular methods are facilitating our understanding of the relative roles of asexual vs sexual means of reproduction in bryophytes (Shaw *et al.* 2002). For example, Derda and Wyatt (1990) measured 38 multilocus genotypes in populations of *Polytrichum commune* (Figure 88-Figure 89). They found that 69% of these genotypes were distributed evenly across the range of the species, with a mean genotypic diversity of 0.546 ± 0.042 . This is a low value, coupled with potential for vegetative reproduction, and Derda and Wyatt used it to support the concept that spore-mediated gene dispersal in this species is limited. Van Zanten (1973) likewise asserted that dispersal of *Dawsonia* (Figure 90), another member of the *Polytrichaceae*, is limited due to the epiphragm that requires physical contact such as a raindrop to expel the spores.



Figure 88. *Polytrichum commune* with capsules. Photo by David Holyoak, with permission.

This chapter will consider each of these diaspore mechanisms and some examples of dispersal types among the bryophytes. Where possible (data are limited), we will examine what contributes to their success in getting established.



Figure 89. *Polytrichum commune* capsule showing epiphragm connected to teeth, forcing spores to exit the capsule from the sides. Photo by Michael Lüth, with permission.



Figure 90. *Dawsonia longiseta* with capsules. Photo by Niels Klazenga, with permission.



Figure 91. *Polytrichastrum formosum*. Photo by Tom Thekathyl, with permission.

Which Strategy Accomplishes More?

In a model designed for Bryozoa, not bryophytes, Karlson and Taylor (1992) provided criteria for dispersal that would seem also to apply to bryophytes. Dispersal involves a tradeoff between energy spent on probable success of short distance dispersal and the energy lost to provide an expansion of the species through long-distance dispersal. "Using a procedure which minimizes the extinction probability for the lineage (hence maximizing survivorship of the genetic individual)," they predicted that "a high proportion of dispersed offspring should be associated with high numbers of asexual offspring, a low risk of mortality to offspring during dispersal, and high local survivorship of offspring."

One consequence of vegetative reproduction and dispersal might be a loss of genetic diversity. Van der Velde *et al.* (2001) used the genetic structure of *Polytrichastrum formosum* (Figure 91) to assess this genetic diversity in sexual vs asexual reproduction. They found that the levels of microsatellite variability were, on average, lower than those known for most other plant species. Nevertheless, genotypic diversity within the populations studied was high. They interpreted this as an indication that sexual reproduction is an important determinant of the within-population genetic structure of *P. formosum*. Furthermore, Van der Velde *et al.* found no significant differences among microsatellite markers between populations or between regions (450 km in Denmark vs the Netherlands). They likewise interpreted this as evidence of sexual reproduction with high effective spore dispersal between populations, despite the well known ability of this species to reproduce clonally, supporting the interpretations discussed above for *Pseudoscleropodium purum* (Figure 6), *Pleurozium schreberi* (Figure 7), and *Rhytidiadelphus squarrosus* (Figure 70) (Fritz 2009). Members of the *Polytrichaceae* do not produce specialized asexual reproductive structures, and reproduction by fragments exists but is poorly known for most of the *Polytrichum/Pogonatum/Polytrichastrum* group (Figure 91).

The leafy liverwort *Orthocaulis attenuatus* (= *Barbilophozia attenuata*; Figure 92) provides another example of the tradeoffs. Korpelainen *et al.* (2011) found that diaspores of this species in the diaspore bank of a forest floor can be activated by disturbance. A disturbance as small as ant trails can favor the establishment of large gemmae over small spores for establishment. They found that these gemmae are effective at short distances, but not at mid-distances. For longer distances, spores are an effective means of dispersal. This short-distance gemmae dispersal provides compatible genotypes already adapted to this environment, but the tradeoff is the lack of genetic diversity and other problems attached to inbreeding.

Lost Energy

Production of sporophytes is a cost in energy. First, it costs energy to produce antheridia and archegonia. Then it costs energy to nourish the sporophyte to maturity. Production of spores likewise costs energy. Therefore, this costly process needs to afford a significant advantage for the species to succeed and survive with this strategy through evolution.



Figure 92. *Orthocaulis attenuatus* (= *Barbilophozia attenuata*), showing gemmae at the tips of some branches. Photo by Michael Lüth, with permission.

Nevertheless, some species seem to produce sporophytes to no avail. Unfavorable conditions for development may make vegetative dispersal more important than dispersal of spores. In Nigeria, the widespread *Bryum coronatum* (Figure 93) produces abundant sporophytes, but it appears that they have a large failure rate (Egunyomi 1982). Among those in the study, 42% remained undehiscent even during the dry season when they normally discharge spores. Furthermore, 41% of the setae never developed capsules. Although the spore germination rate was 65-88%, protonemal growth was abnormal. The abundant production of axillary propagules is certainly important in those seasons, most likely frequent, when conditions during sporophyte development are less than ideal. This is a widespread species and sporophytes are most likely more important in other locations where conditions are more favorable for them.



Figure 93. *Bryum coronatum*, a moss with a large failure rate for sporophytes in Nigeria. Photo by Jan-Peter Frahm, with permission.

As already mentioned, for species that produce large numbers of spores that travel great distances, most of those spores will not reach a suitable substrate and microclimate, hence contributing to the loss of energy.

Liverworts vs Mosses

Longton (1997) pointed out that the production of specialized asexual propagules is more common among (leafy) liverworts than among mosses. Gemmae are so common among leafy liverworts that their species often are identified by the structure and location of their gemmae. In the British liverwort flora, Laaka-Lindberg *et al.* (2000) found no association between production of asexual propagules and rarity, or with the monoicous vs dioicous condition. But those species that produce neither spores nor special asexual propagules are typically rare.

Habitat Differences

Disturbed Habitats

Disturbance can play a selective role for species that may be mediated by tradeoffs between dispersal rate and establishment success. Kimmerer (1993) found that *Tetraphis pellucida* (Figure 94-Figure 95) benefitted from frequent disturbance, whereas suppressed disturbance caused it to become out-competed by other bryophytes. Its competitor, *Orthodicranum flagellare* (Figure 96), is

successful in colonizing gaps when there are other populations of the species nearby to contribute asexual brood branches. These germinate more rapidly than the gemmae of *Tetraphis pellucida* (Figure 94-Figure 95), making *O. flagellare* the better competitor.



Figure 94. *Tetraphis pellucida* gemmae in splash cups. Photo by Jan-Peter Frahm, with permission.

Flood plains, arable fields, and other regularly disturbed habitats are colonized by species that can lie dormant in diaspore banks during periods unsuitable for growth, or they must arrive quickly, colonize immediately, and complete their life cycles before the habitat is once again unfavorable. Such a habitat favors such species as thallose liverworts that can roll up their thalli, dry out, and resume growth from dormant terminal buds, as in *Riccia* (Figure 97). These are often invisible to the naked eye until those suitable growth conditions are provided, either in the field or in the lab. Kürschner and Parolly (1999) found that this community in Turkey consisted mostly of annual shuttle species and vegetative colonists that produced very large spores, retained spore tetrads, and/or produced asexual propagules, all of which survived in the diaspore bank during winter flooding and were able to re-establish the community quickly when the flood waters receded.

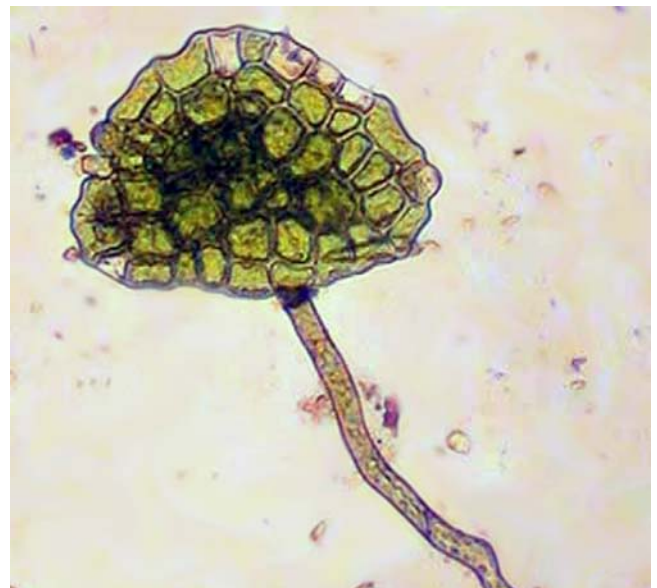


Figure 95. *Tetraphis pellucida* gemma germinating. Photo from UBC botany website, with permission.



Figure 96. *Orthodicranum flagellare* showing flagelliform branches that serve as propagules. Photo by Jan-Peter Frahm, with permission.



Figure 97. *Riccia bischoffii* var. *ciliifera* on drying mud. Photo by Jan-Peter Frahm, with permission.

Bijlsma *et al.* (2012) found *Ephemerum cohaerens* (Figure 98) and *E. serratum* var. *rutheanum* (Figure 99) in extensive beds where there was regular inundation and high flooding until May or early June, hence causing a setback to competing vegetation. They attributed the success of these species in these conditions to the flooding, life strategy, and soil characteristics. The large spores and tubers permitted these species to remain in the diaspore bank, whereas the rapid development of an extensive protonemal mat following the recession of flood waters gave them an establishment advantage. Their short life cycle permitted them to form plants in late summer and complete the life cycle to spore production in autumn.



Figure 98. *Ephemerum cohaerens* with perigonia. Photo by Dick Haaksma, with permission.



Figure 99. *Ephemerum serratum* with capsules. Photo by David T. Holyoak, with permission.

Arable fields are a man-made habitat that favors certain bryophyte species. This can be a suitable habitat for some members of the **Anthocerotophyta**, but changes in agricultural practices can make the habitat unsuitable. Following years of hornwort-unfriendly agricultural practices, new eco-friendly practices returned in some areas of Europe. Bisang *et al.* (2009) compared the presence of this hornwort group before and after the eco-friendly practices were established in the Swiss plateau and found the return of *Anthoceros agrestis* (Figure 100) and *Phaeoceros carolinianus* (Figure 101-Figure 102). The re-establishment of these two species apparently resulted from spores that remained persistent in diaspore banks through the many years of unfavorable conditions.

Other disturbed habitat colonizers, like *Marchantia* (Figure 103), are frequent in the diaspore rain (Gaur & Kala 1984; Ross-Davis & Frego 2004) and arrive almost continuously, ready to take advantage of the low competition. *Marchantia polymorpha* is one of the colonizers after a forest fire (Graff 1936). In their experiments on buried propagules in an old-growth forest, Ingersoll and Wilson (1990) found that most (88%) of the gametophores emerging were from vegetative sprouts. There were significantly more vegetative sprouts in the undisturbed treatments. The number of emergents responded inversely to an increase in disturbance, with exposure to sun causing a significant decline in the six most abundant species. Vegetative structures with shallow burial were lost in the fire treatment.



Figure 100. *Anthoceros agrestis* with splitting sporophytes exposing spores. Photo by Michael Lüth, with permission.



Figure 101. *Phaeoceros carolinianus* on disturbed soil. Photo by Michael Lüth, with permission.

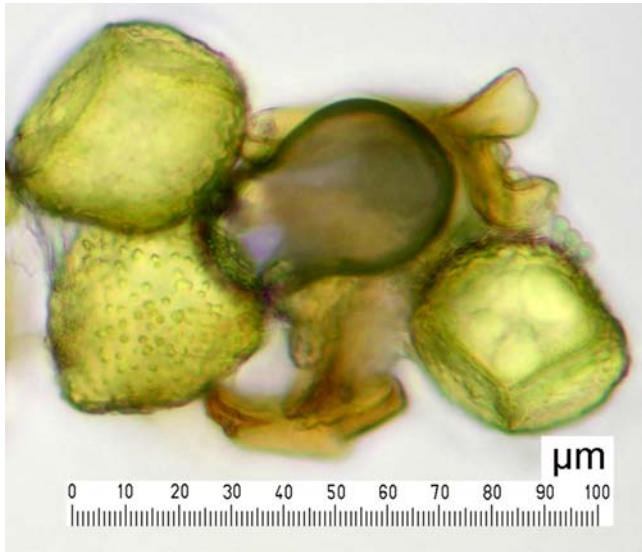


Figure 102. *Phaeoceros carolinianus* spores. Photo by David Wagner, with permission.

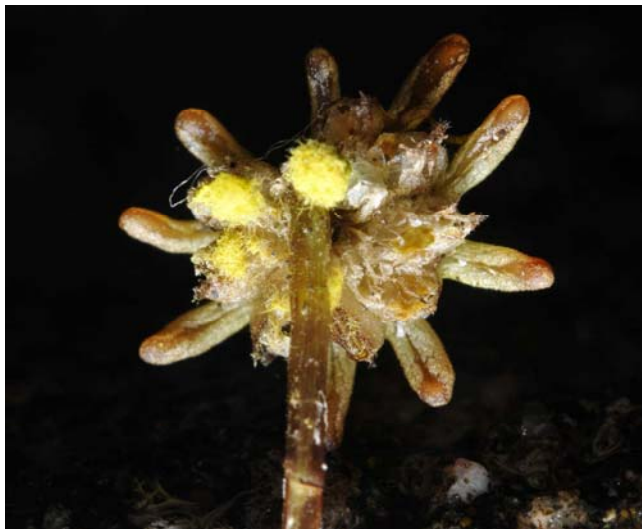


Figure 103. *Marchantia polymorpha* archegonial head showing spores and elaters. Photo by George Shepherd, through Creative Commons.

Unfortunately, our methods of determining what is in either diaspore banks or diaspore rain requires culturing, and this method is both time-consuming and incomplete, permitting us to identify the species if growth to a gametophore is successful, but often not permitting us to

identify the dispersal structure that produced it. And we might not provide the right conditions for its successful development.

Epiphytes

Löbel and Rydin (2009) found that in epiphytic bryophytes, the conditions in the habitat influenced the production of sporophytes, but not that of asexual propagules. Furthermore, development of sporophytes had a negative effect on growth, whereas presence of asexual propagules did not. Further detriments to the sexual strategy arise from the need to reach a certain colony size before reproduction is effective; there is no threshold for the asexual reproduction. Thus, two sets of trade-offs arise: dispersal distance vs reproductive age and dispersal distance vs sensitivity to habitat quality. They considered that habitat turnover and connectivity may be more important selection pressures than species interactions.

The genus *Radula* (Figure 104), a leafy liverwort in which both monoicous and dioicous taxa exist, demonstrates a specific case for the advantages of asexual reproduction. In this genus that lives in a frequently dry environment, there was no correlation with either dioicy or epiphytism (Devos *et al.* 2011). Rather, there seems to have been a shift from sexual systems (dioicy to monoicy) among the facultative epiphytic taxa several times. Both facultative and obligate epiphytes in this genus produce gemmae equally, as well as dispersing gametophyte fragments. These asexual propagules may provide a pre-adaptive mechanism that permits the facultative epiphyte taxa to live on trees where frequent wetting and drying out are detrimental to the development of protonemata into buds and gametophores. Fragments and asexual propagules can skip this stage or use it only briefly before developing into a leafy plant. Devos *et al.* suggest that the larger size of these diaspores imposes a tradeoff by limiting dispersal distance.



Figure 104. *Radula lindenberghiana* with gemmae. Photo by Jan-Peter Frahm, with permission.

Peatlands

Peatlands are unique habitats, and they seem to do lots of things differently. Poschlod (1995) examined the relative importance of spores and fragments in the recolonization of milled peatlands in the Bavarian foothills of the Alps. He found that spores were relatively unimportant in the diaspore rain, but that fragments did

appear in the spore traps. In particular, branches and leaves of *Sphagnum magellanicum* (Figure 55), *S. capillifolium* (Figure 47), and *Polytrichum strictum* (Figure 45) were captured in the traps in most of the study sites. Furthermore, diaspore bank samples were placed in pots and cultivated for more than one year. In these pots, only three species germinated and grew: *Betula* (birch tree), *Marchantia polymorpha* (Figure 103), and *Funaria hygrometrica* (Figure 164).

The Antarctic

Harsh environments impose different selection pressures from the ones at play in more friendly environments. Lewis Smith and Convey (2002) offered evidence to refute the long-held hypothesis that bryophyte fertility decreases as latitude (and climate severity) increases. Using the maritime Antarctic (68-72° S lat) as an example, they demonstrated that a relatively high proportion of the bryophytes there were capable of producing sporophytes. At Marguerite Bay, 43% of the species (17 species of mosses, 2 of liverworts) were known to produce sporophytes; at Alexander Island it was 47% (16 species of mosses, 1 of liverworts). In more arid parts of the Antarctic continent, the number was less (33%). This is still considerably smaller than that found by González-Mancebo and Hernández-García (1996) for an altitudinal gradient in the Canary Islands, where most life cycle strategies had 70% fertility, with that of the perennial stayers being lower.

Not surprisingly, Lewis Smith and Convey (2002) found that most of the Antarctic fertile mosses in their study areas were short, monoicous acrocarpous species. For dioicous species, the problem arises of having both genders arrive on the island in sufficient proximity and having both mature at the same time under a different set of temperatures, day length, and moisture regime than at their source.

In this harsh Antarctic environment, spores were more abundant than bryophyte fragments in the Rotorod® samplers of Signy Island (Marshall & Convey 1997). Spore size did not seem to matter, with all five taxa occurring in samples 0.5-1 km from their nearest known sources. Nevertheless, the presence of spores was small compared to their represented ground cover and in comparison to the lichen propagules in the same samples. This extensive ground cover most likely resulted from vegetative spread after spore arrival.

Plasticity of Spore Size

Habitat may matter as well in determination of successful spore size and means of reproduction within a species. Hassel and Söderström (2003) compared the spread of *Pogonatum dentatum* (Figure 105) in the mountains vs lowlands in Fennoscandia. The lowland plants seem to have a tendency to produce more but smaller spores (statistically non-significant) compared to the mountain plants. Nevertheless, establishment in the mountains seems rarely to occur from either spores or leaves whereas these two methods are frequent in the lowland. On the other hand, the diaspore bank is more important in the mountains because of the more regular and shorter disturbance intervals there. The diaspores of *P.*

dentatum are apparently too short-lived to survive the longer disturbance intervals in the lowlands.



Figure 105. *Pogonatum dentatum*. Photo by Jan-Peter Frahm, with permission.

Seasons

In a study of airborne pollen and spores in Buenos Aires, Noetinger *et al.* (1994) noted that while spores are scarce throughout the year, they are mainly represented by the bryophytes, with the greatest densities in May to June. For seed plants, pollen density was dependent on phenology of the species, and densities corresponded with blooming seasons of the various groups. Latorre *et al.* (2008), in Mar del Plata city, Argentina, found an increase in pollen with an increase in temperature, reaching a maximum in early spring. Data differed among the trap types, with a negative correlation with wind using the Burkard trap and negative correlation with humidity using the Tauber trap. Data supporting such correlations with phenology and weather for bryophytes are meager. And some bryophytes retain their capsules for more than one year.

Marshall and Convey (1997) were surprised to find that spores were captured over a long time period on Signy Island in the Antarctic, including captures in the winter months. With availability of bare substrate, it is possible that spores could be redistributed from non-trapping surfaces throughout the year. Just what is going on during the seasons when most of us are not looking?

For *Polytrichastrum ohioense* (Figure 106) in the subalpine zone of the Yatsugatake Mountains, Central Honshu, Japan, capsules endure the winter in an immature stage, taking 13 months to mature and dispersing their spores in the following mid-July to mid-August (Ayukawa *et al.* 2002). In *Racomitrium africanum* (Figure 107), *Fissidens weirii* (as *Fissidens glauculus*), *Thuidium gratum*, and *Stereophyllum* sp. (Figure 108) in southwest Nigeria, sporophytes develop and mature at the end of the same rainy season (Oct/Nov & Dec) as that for fertilization (beginning of rainy season) (Odu 1981). Spores from mature capsules of these species all dispersed during and after the dry season (Nov-Apr).

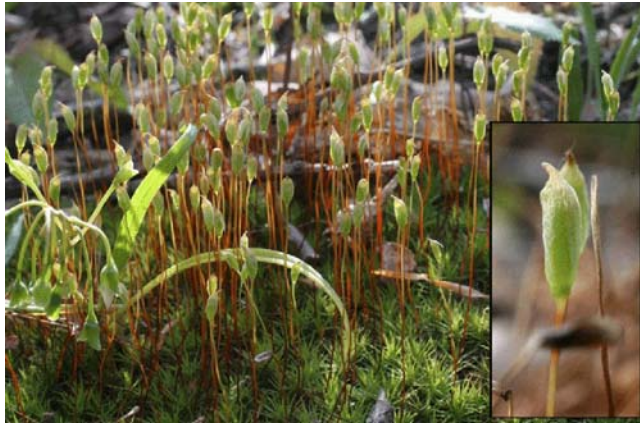


Figure 106. *Polytrichastrum ohioense* with capsules that take more than one year to mature. Photos by Bob Klips, with permission.



Figure 107. *Racopilum africanum* with developing sporophytes. Photo by Jan-Peter Frahm, with permission.



Figure 108. *Stereophyllum radiculosum* on bark. Photo by Scott Zona, through Creative Commons.

For *Archidium ohioense* (Figure 109), *Bryum coronatum* (Figure 93), *Fissidens minutifolius*, and *Trachycarpidium tisserantii*, also in southwest Nigeria, capsule dehiscence and spore dispersal occurred in September – October (Makinde & Odu 1994). But in this case, the stages of sporophyte development occurred during the rainy season, including capsule dehiscence and falling

of the capsules themselves. Not surprisingly, they found that the spores did not discharge easily from the cleistocarpous capsules of *A. ohioense* or *T. tisserantii*. In the Hiruzen Highlands of Japan, Nishimura (1993) found that dispersal dates for 34 species of mosses occurred in late autumn (late November) to early spring (early April); 12 occurred in late spring to summer (May to August) and 5 in autumn (September to November). One had no definite season and one had two dispersal seasons. In these examples, it appears that the season of dispersal is not random, but that conditions needed for one species may not be suitable for another. It is easy to understand that most small spores will benefit from dispersal when it is dry, permitting them to be carried by wind and air currents to new locations. For those with large spores that fall to the ground, a rainy season is beneficial for immediate germination and growth.



Figure 109. *Archidium ohioense* with capsules. Photo by Li Zhang, with permission.

Time of day matters and may help us to unravel the conditions favoring dispersal. For pollen, Pérez *et al.* (2003) found a maximum between 10:00 and 12:00 h, with a minimum at 18:00 h in Mar del Plata, Argentina. They suggested that optimal diurnal conditions for dispersal of arboreal pollen are high temperatures and low relative humidity. It is likely that this relationship could be applied on an annual scale and that it would also apply to bryophyte spores.

One seasonal advantage of asexual propagules is that they are generally produced throughout the growing season, whereas spores tend to be released during a limited time each year (During 2001).

Are These Adaptations?

Capsules and Setae

Setae develop first in **Bryophyta** and last in **Marchantiophyta** relative to the capsule. In either case, the elongated seta extends the spores farther above the plant (Figure 110), increasing the chances for them to be dispersed. Even in the **Anthocerotophyta**, where there are no setae, the elongate sporophyte matures from top down and dispels its spores from the top (Figure 100). Hence, we

might expect some differences in the length of the setae, with longer setae permitting spores to get farther from the parent bryophyte, and perhaps even hornwort sporophyte lengths, relative to dispersal needs. These may or may not correlate with characters of the capsule itself.



Figure 110. *Pohlia nutans* with nodding capsules and long setae. Photo by Michael Lüth, with permission.

We can list a number of differences among capsules that might contribute to their dispersal ability. Paramount among these is the means by which the capsule opens and dispels the spores. These will be discussed in some detail in the ensuing paragraphs, but one we might consider first is the drying of the capsule interior prior to spore expulsion. This process and its importance seem to lack experimentation except in *Sphagnum* (Figure 47-Figure 52), so some speculation is in order. Chater *et al.* (2011) have cited the regulation of stomatal behavior in photosynthetic organisms for 400 million years of evolution. Its role in leaves of tracheophytes is clear, but in bryophytes the sporophyte tissue is not in a leaf, and it is the sporophyte capsule that has the stomata (Renzaglia *et al.* 2000). However, it appears that as in the leaf, this tissue controls (perhaps permits is more appropriate) the loss of water. Recent evidence proposed by Duckett *et al.* (2010) suggest that we should consider the possible role of stomata in permitting the escape of moisture from the capsules of other mosses (Figure 111). Such drying leads to changes in capsule shapes and can contribute to the loss of the operculum, sometimes quite forcibly. This aspect of dispersal will be discussed in detail in another subchapter (4-9), but it may be helpful to keep this potential role in mind here as we examine dispersal strategies.

Habitat Differences

Spore capsules in mosses (but not in liverworts) seem to differ considerably among species, and many of these seem to fall into habitat categories. As Vitt (1981) points out, the function of the sporophyte is to produce and disperse the spores as efficiently as possible. In this role, selection pressures should shape the sporophyte into the most effective organ for its growing conditions. These selective pressures differ significantly among the major habitat classifications of hygrophytic, mesophytic, and xerophytic.

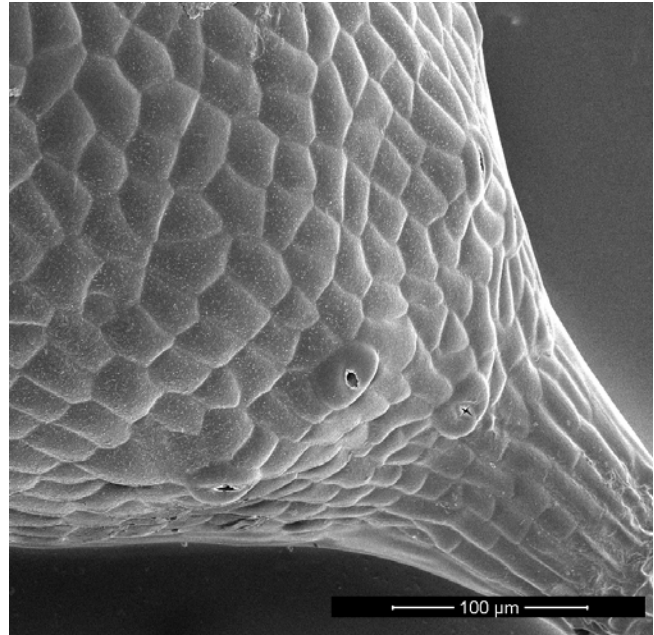


Figure 111. SEM of *Physcomitrella patens* stomata at base of capsule. Photo courtesy of Jeff Duckett and Silvia Pressel.

Xerophytes may be characterized by reduction of the sporophyte, including shorter seta length, broader and erect capsules, reduced or absent peristome including cleistocarpy, and large spores (Vitt 1981). These characters are often accompanied by a shortened life cycle that permits the xerophytes to avoid extended dry periods. As evidence, Vitt points out that this same group of adaptations has evolved in a number of unrelated mosses, including the acrocarpous genera *Bryobartramia*, *Viridivellus*, *Sporledera* (Figure 112), *Goniomitrium* (Figure 113), and pleurocarpous genus *Gigaspermum* (Figure 114). Others, including *Encalypta brevipes* (Figure 115), *Ditrichum* spp. (Figure 116), *Funaria* spp. (Figure 117), *Pottia* (Figure 118), *Stegonia* (Figure 119), *Trematodon* (Figure 120), and *Weissia* (Figure 121), lack the reduced life cycle but exhibit the other xerophytic adaptations.



Figure 112. *Cleistocarpidium palustre* (= *Sporledera palustris*) showing broad capsules. Photo by Jan-Peter Frahm, with permission.



Figure 113. *Goniomitrium acuminatum* subsp. *enerve*, demonstrating the broad capsule typical of a xerophyte. Photo by David Tng <<http://www.davidtng.com/>>, with permission.



Figure 114. *Gigaspermum repens*, demonstrating the broad capsule typical of a xerophyte. Photo by David Tng <<http://www.davidtng.com/>>, with permission.



Figure 116. *Ditrichum subulatum*, a species with an expanded capsule urn relative to others in the genus. Photo by Des Callaghan, with permission.



Figure 115. *Encalypta brevipes* Khibiny Mountains, Apatity, Murmansk. Photo by Michael Lüth, with permission.



Figure 117. *Funaria pulchella* showing expanded capsule urn. Photo by Michael Lüth, with permission.



Figure 118. *Pottia conica*, showing capsules with expanded urn. Photo by Jan-Peter Frahm, with permission.



Figure 119. *Stegonia latifolia* with slightly rounded capsules. Photo by Michael Lüth, with permission.



Figure 120. *Trematodon longicollis*, a moss of disturbed banks. Note the long neck and expanded urn. Photo by Li Zhang, with permission.



Figure 121. *Weissia controversa* var. *densifolia* showing swollen urn. Photo by Barry Stewart, with permission.

Mesophytic taxa, on the other hand, can have amplified capsules, as in the entomophilous members of the **Splachnaceae** (Vitt 1981; Figure 185). Vitt lists other taxa exhibiting sporophytic amplification are some **Dicranaceae** (as polysety; Figure 122), **Mniaceae** (Figure 124), **Hypnodendraceae** (Figure 123), and **Dawsonia** [amplified peristome (Figure 126) compared to other **Polytrichaceae** (Figure 89)]. The mesophytic group, not faced with the extremes of habitat, has taken multiple routes that preclude a clear definition of adaptations. Vitt (1979, 1981) included elongate, straight setae; curved, horizontal to pendent capsules that are smooth, cylindric, and have well-developed peristomes as common characters of mesic forest floor mosses. Example taxa include *Plagiomnium cuspidatum* (Figure 124) and *Timmia megapolitana* (Figure 127).



Figure 122. *Dicranum polysetum* with polysetous capsules. Photo by Janice Glime.



Figure 123. *Hypnodendron commutatum* showing the large capsule. Photo by Janice Glime.



Figure 125. *Cladomnion ericoides* from Pureora Forest, Taupo, NZ. Photo by Andy Hodgson, with permission.

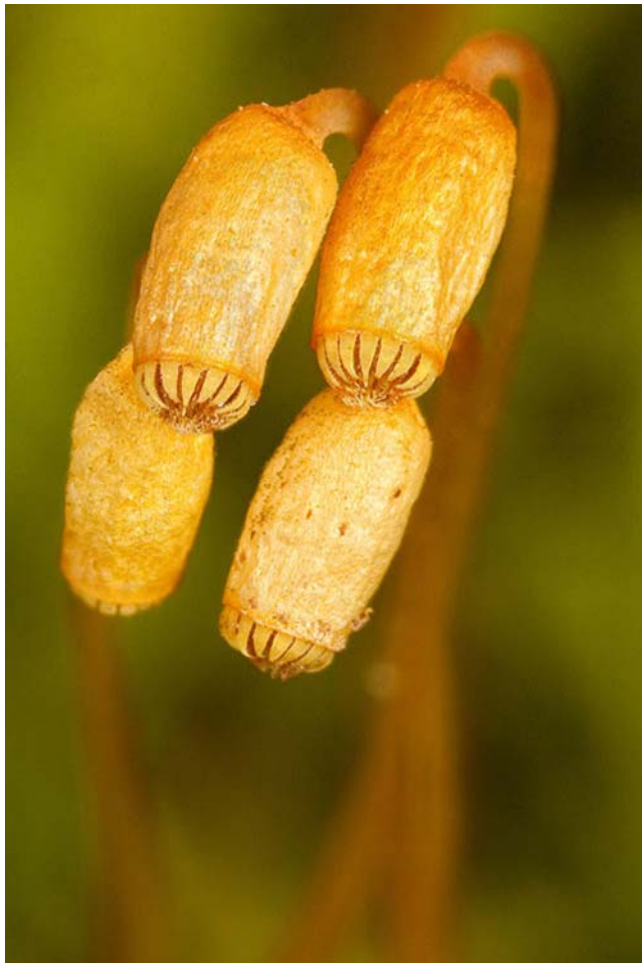


Figure 124. *Plagiomnium cuspidatum* illustrating the straight setae with smooth, cylindric, pendent capsules and well developed peristomes. Photo by Robert Klips, with permission.



Figure 126. *Dawsonia longifolia* capsule showing enlarged teeth. Photo from University of British Columbia Botany website, with permission.



Figure 127. *Timmia megapolitana*. Photo by Jessica M. Budke, with permission.

Epiphytes usually have xerophytic adaptations, but these differ from those of the edaphic species because dispersal is a different problem for these elevated taxa. *Cladomnion ericoides* (Figure 125) provides a good example of epiphytic adaptations with its short, stout setae (permitting leaves and perichaetial leaves to protect the capsule from desiccation); erect, ribbed, ovate-oblong capsules; and sheathing perichaetial leaves (Vitt 1981).

Many epiphytic members of the **Isobryales** share similar features with other bryophytes of vertical surfaces: *Haplohymenium* (Figure 128), *Andreaea* (Figure 129), *Fabronia* (Figure 130), *Grimmia* (Figure 183), *Tortula* (Figure 131), *Hedwigia* (Figure 132), *Orthotrichum* (Figure 133-Figure 135), *Ptychomitrium* (Figure 136), *Racomitrium s.l.* spp. (Figure 137), and *Tortella* (Figure 76), presumably adapting them to vertical substrates where humidity alternates between dry and wet periods and light intensity is higher (Vitt 1981). These habitat characteristics seem to favor the short, erect, ribbed capsules; short, stout

setae; reduced peristomes; and sheathing perichaetial leaves. Epiphytic *Orthotrichum*, on the other hand, seems to have evolved from ribbed [e.g. mesophytic *O. lyellii* (Figure 133) or *O. vittii* (Figure 134)] to smooth [e.g. xerophytic *O. pusillum* (Figure 135)] capsules (Vitt 1981).



Figure 128. *Haplohymenium triste* with lichens on bark. Photo by Bob Klips, with permission.



Figure 129. *Andreaea rothii* subsp. *falcata* showing valvate cylindric capsule. Photo by Barry Stewart, with permission.



Figure 130. *Fabronia ciliaris* with ovate capsules and short setae. Photo by Michael Lüth, with permission.



Figure 131. *Tortula canescens* capsules showing cylindrical shape and extended spiral peristome. Photo by Des Callaghan, with permission.



Figure 132. *Hedwigia ciliata* with short capsules on short setae and surrounded by perichaetial leaves. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.



Figure 133. *Orthotrichum lyellii* with gemmae. Photo by Jonathan Sleath, with permission.



Figure 136. *Ptychomitrium polyphyllum* showing short seta and cylindrical capsule. Photo by Malcolm Storey at Discover Life, through Creative Commons.



Figure 134. *Orthotrichum vittii* showing ribs on capsule. Photo by Jan-Peter Frahm, with permission.



Figure 137. *Bucklandiella affinis* (= *Racomitrium affine*) with cylindric capsules, reduced peristome, and short setae. Photo by Michael Lüth, with permission.



Figure 135. *Orthotrichum pusillum* capsules. Note the nearly smooth (non-ribbed) surface of these capsules. Photo by Bob Klips, with permission.

Vitt (1981) considers two groups of mosses with submerged or emergent habits. Those with aquatic gametophytes and terrestrial sporophytes, often produced at times of low water levels, include, for example, *Scorpidium* (Figure 138), *Hygrohypnum* (Figure 139), *Platylomella* (as *Sciaromium*; Figure 140), *Drepanocladus* s.l. (Figure 142), and *Platyhypnidium riparioides* (Figure 141). These taxa have sporophytes that align with mesophytic bryophytes from the forest floor. On the other hand, the aquatic mosses with aquatic sporophytes [e.g. *Blindia* (Figure 143), *Fontinalis* (Figure 144), *Wardia* (Figure 145), *Scouleria* (Figure 146)] tend to have reduced or absent peristomes; ovate or oblong, smooth, immersed capsules; enlarged perichaetial leaves; and thick or leathery **exothecial** (outer capsule wall) cells.

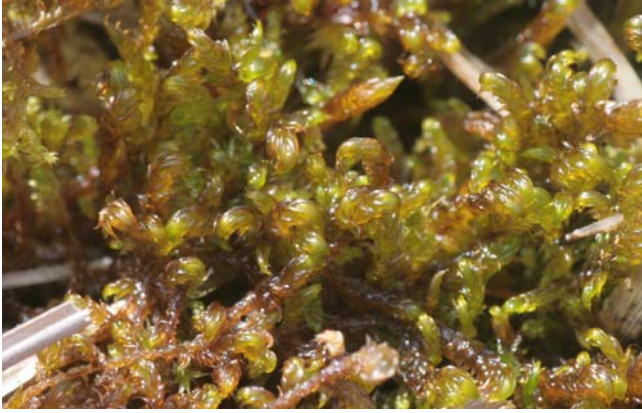


Figure 138. *Scorpidium cossonii*. Photo by Hermann Schachner, through Creative Commons.



Figure 139. *Hygrohypnum luridum* with emergent capsules. Photo by Michael Lüth, with permission.



Figure 140. *Platylomella lescurii*, a species that produces capsules at low water levels. Photo by Blanka Shaw, with permission.



Figure 141. *Platyhypnidium riparioides* showing emergent capsules. Photo by Andrew Hodgson, with permission.



Figure 142. *Warnstorfia* (previously *Drepanocladus*) *fluitans* with capsules. Photo by Biopix, through Creative Commons.

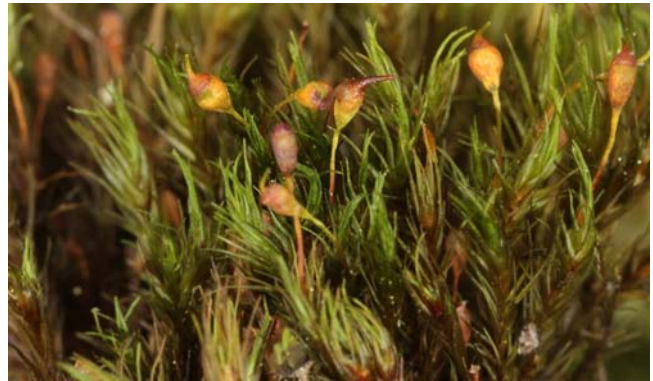


Figure 143. *Blindia acuta* showing ovate capsules common among submersed species. Photo by Jan-Peter Frahm, with permission.



Figure 144. *Fontinalis squamosa*, member of a genus that produces submersed, ovate, thick-walled capsules that have short stalks and enlarged perichaetial leaves. Photo by David Holyoak, with permission.



Figure 145. *Wardia hygrometrica* from the southwest Cape of Africa, showing oblong capsules typical of submersed species. Photo by Des Callaghan, with permission.



Figure 146. *Scouleria aquatica* with a submersed capsule typical of aquatic species. Photo by Matt Goff <<http://www.sitkanature.org/>>, with permission.

Anisospory

Mogensen (1981) points out that having **anisospory** (unequal spore sizes, in this case) creates different dispersal potential between males (small spores) and females (large spores). One would presume that small spores will disperse farther, hence making it more likely that males establish as single-sex populations in distant places. It also seems that there is an advantage in the production of dwarf males from these anisosporous male spores because some

of these will germinate on a female and thereby be close enough to accomplish fertilization. There is no equivalent advantage for the female spores to land on another member of the species because these are never known to produce dwarf plants that might somehow accomplish fertilization. Rather, in most cases, they will not germinate at all when landing on their own genotype.

Spores and Spore Walls

Liverworts and mosses differ in the number of layers in the spore wall (Mogensen 1981). Both have **intine** and **exine**. The **intine** (Figure 147) is the inner wall and possesses the aperture that is responsible for the breakup of the spore wall during germination. The **exine** is the outer wall and thus protects the spore from the environment. The **perine** is present only in moss spores and is laid down on the outer surface of the spore. It is not produced by the spore, but rather, the surrounding sporophyte deposits the perine (Figure 148) material on the spore walls. This perine is of taxonomic value and one might assume that it has environmental significance, but little information is available to provide us with such correlations.

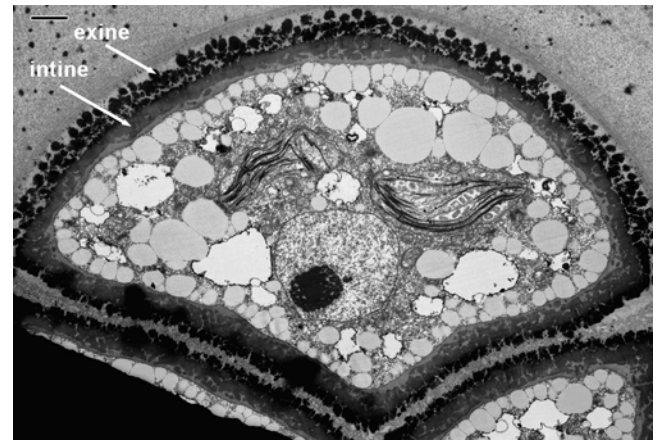


Figure 147. *Andreeaea rothii* TEM of spore. Photo courtesy of Karen Renzaglia.

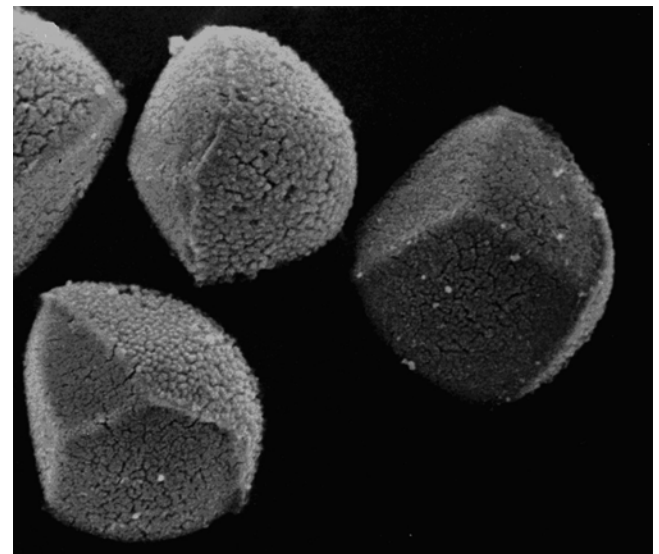


Figure 148. *Andreeaea rothii* spore SEM showing papillae (perine layer) laid down by the sporophyte. Photo courtesy of Karen Renzaglia.

Some speculation is in order so that we can develop hypotheses about this perine layer (Figure 148). This layer causes air to be trapped in spaces around the surface of the spore. So one hypothesis is that the spores trap air that makes them lighter in weight per unit volume, permitting them to float. What are the advantages gained by spaces so small that cohesion of water molecules prevents them from entering those spaces? Does this potential repellence of water prevent inappropriate germination? And what difference does the pattern make? Or could it be that this layer provides a food source for potential dispersal agents that pass the spore through the gut unharmed at some new location or simply carry the spores like ants do seeds with elaiosomes? Does the layer have any food value? Does it make adherence easier for both dispersal and attachment to substrate?

Liverworts

Bischler and Jovet-Ast (1981) contend that adaptations in liverworts are primarily those of biochemical and biophysical properties of the cell content, hence making them more difficult to assess. Both the gametophyte and sporophyte produce specific **flavonoids** that may protect the developing gametes and spores from UV light (Suire & Asakawa 1980). They likewise synthesize secondary compounds that seem to deter predators and parasites. SEM images provided by William T. Doyle seem to provide evidence that they are also adapted by differences in the sculpturing of the spore wall (Figure 149-Figure 154).

Although liverworts lack a perine layer, spores of many species are not without decoration (Figure 149-Figure 154). Some of the leafy liverworts, e.g. *Frullania chevalieri* (Figure 152), have quite intricate and interesting patterns of papillae; others have deep sculpturing, as in *Fossombronia* (Figure 154).

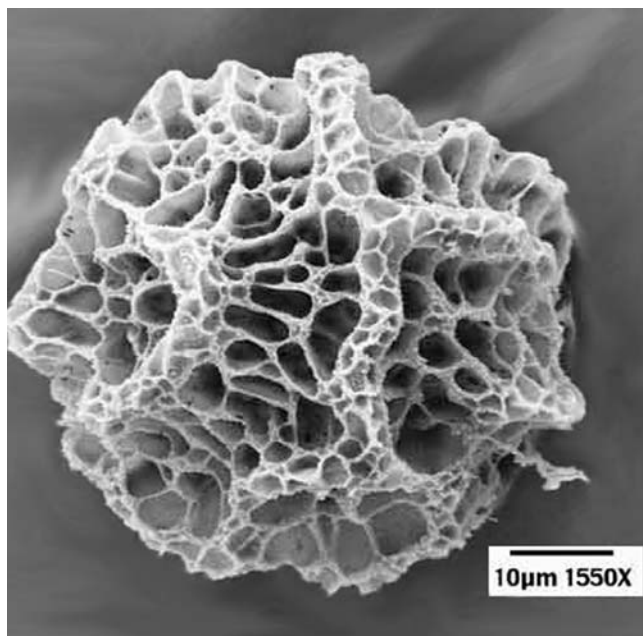


Figure 149. *Targionia hypophylla* distal spore wall SEM. Photo by William T. Doyle, with permission.

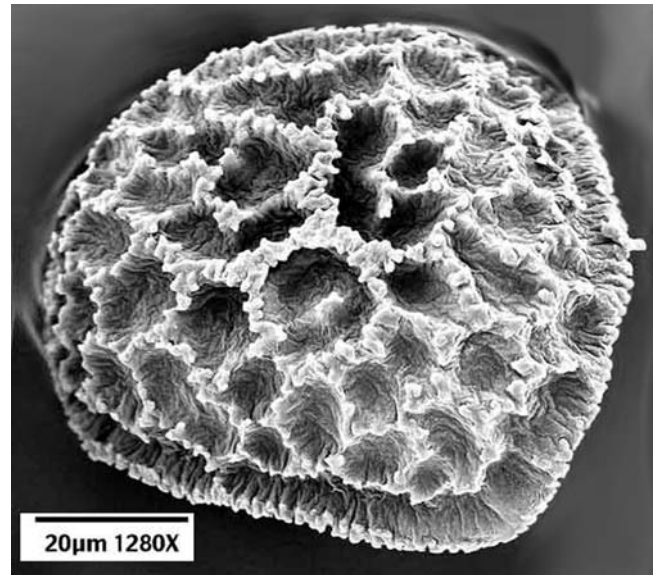


Figure 150. *Riccia cavernosa* distal spore wall SEM. Photo by William T. Doyle, with permission.

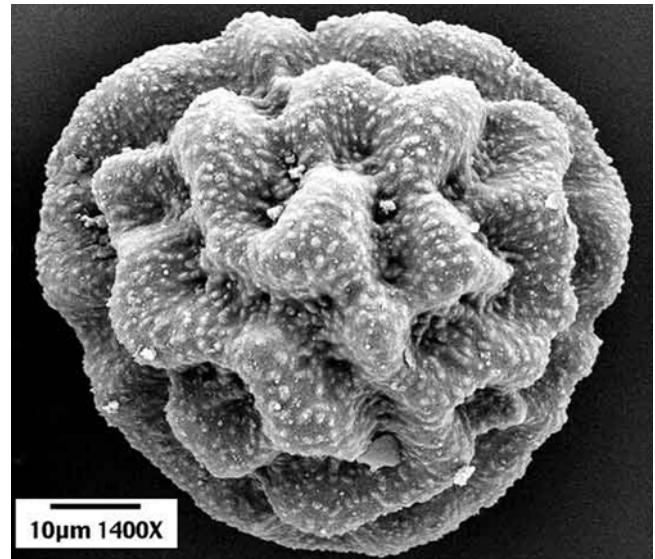


Figure 151. *Mannia californica* distal spore wall SEM. Photo by William T. Doyle, with permission.



Figure 152. *Frullania chevalieri* spore SEM showing the rosettes of papillae. Photo by Matt von Konrat, with permission.

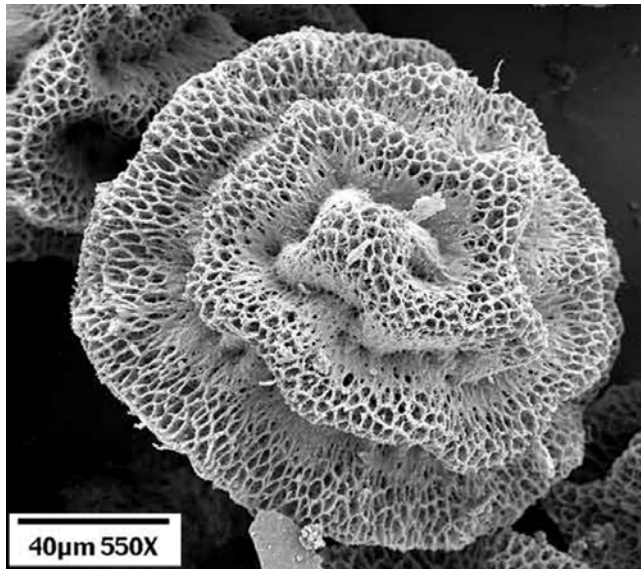


Figure 153. *Asterella californica* distal spore wall SEM. Photo by William T. Doyle, with permission.

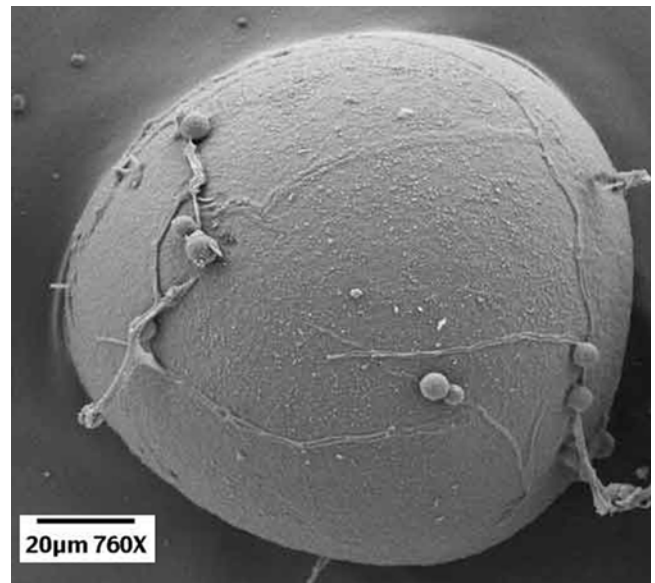


Figure 155. *Geothallus tuberosus* (Sphaerocarpaceae) spore SEM, a species of hot deserts. The large size and smooth surface are typical of spores that don't require adherence on their landing surfaces. Photo by William T. Doyle, with permission.

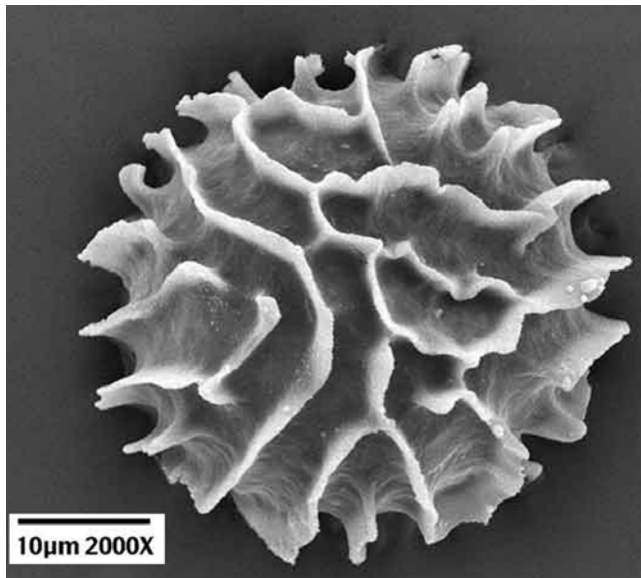


Figure 154. *Fossombronina pusilla* distal spore wall SEM. Photo by William T. Doyle, with permission.

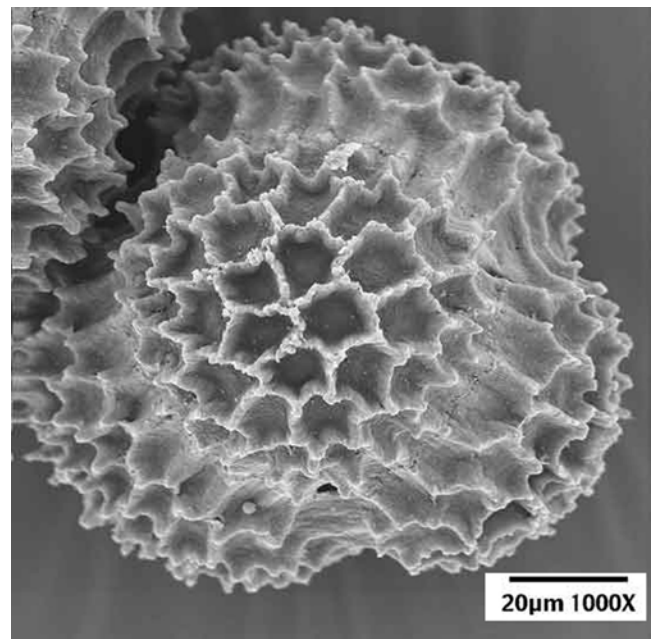


Figure 156. *Sphaerocarpos michelii* distal spore wall SEM. This species lives on damp soil of fallow fields, soils subject to seasonal flooding, and sandy soil of tall-grass prairies. Photo by William T. Doyle, with permission.

But what is the overall indication of these sculpturings? Van Zanten and Gradstein (1988) found no significant difference between the spore sculpturing of transoceanic and endemic Neotropical liverwort species, with both smooth (Figure 155) and finely **verrucose** (covered with warts or wart-like projections) spores (Figure 152) in both groups. On the other hand, they found that there were significantly more strongly verrucose spores among endemic species than among transoceanic species, regardless of size. Furthermore, species with strongly verrucose spores (Figure 156) are typically hygrophytic and terrestrial (a combination for species that live where they are submersed for short periods of time), suggesting to van Zanten and Gradstein that this sculpturing might aid in short-distance dispersal overland by water movements during heavy rainfall. Such a strategy could be useful for *Sphaerocarpos michelii* (Figure 156).

Bischler and Jovet-Ast (1981) attempted to assess reproductive adaptations for the **Marchantiales**. This group is characterized by large spores with an ornamented exine (e.g. *Asterella*; Figure 157). Few species of **Marchantiales** have specialized gemmae [e.g. *Marchantia* (Figure 1), *Lunularia* (Figure 158), *Blasia* (Figure 159) as exceptions], although these are common among leafy liverworts. The sporophyte is imbedded in or surrounded by gametophyte tissue, where it remains until the spores ripen. For many of the taxa, an archegoniophore is produced, hence raising the ensuing sporophyte above the thallus.

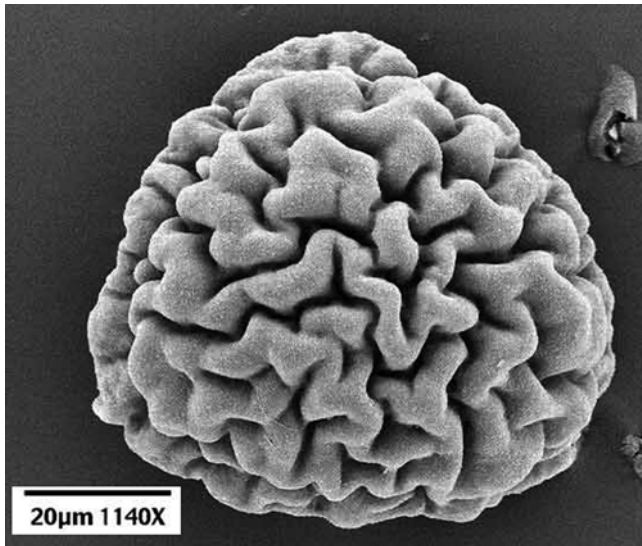


Figure 157. *Asterella palmeri* distal spore wall SEM, illustrating the highly decorated exine and large size. Photo by William T. Doyle, with permission.



Figure 158. *Lunularia cruciata* showing gemmae. Photo by Martin Hutten, with permission.

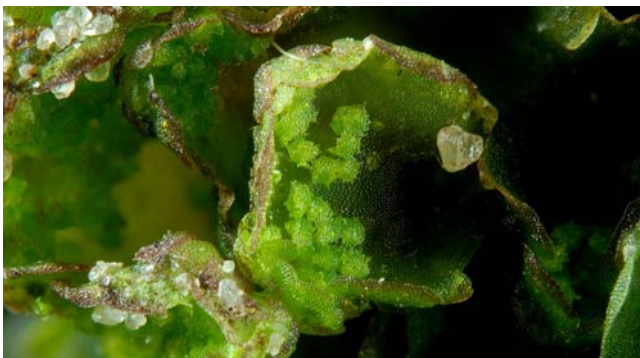


Figure 159. *Blasia pusilla* gemmae on the thallus surface. Photo by Dick Haaksma, with permission.

Elaters occur among the spores of both **Jungermanniales** and **Marchantiales**. These elongate structures twist in response to moisture changes and help in the dispersal in many of the taxa – or do they hinder it by entangling the spores (Figure 160) and forcing them to be dispersed as a mass? Little is known about the role of these elaters in dispersal – perhaps their primary role is in maintaining moisture in the capsule during spore development.



Figure 160. Open capsule of *Jungermannia* sp. showing spores and entangling elaters. Photo by George Shepherd, through Creative Commons.

Monoicous vs Dioicous

One interesting result of the study by van Zanten and Gradstein (1988) is that among the Neotropical liverworts they considered, monoicy vs dioicy made a difference in dispersal. Gradstein (1985) found that 57% of the endemic **Lejeuneaceae** (Figure 161-Figure 162) are monoicous. In the **Jubulaceae** (Figure 163), only one transoceanic species is dioicous. Van Zanten and Gradstein (1988) concluded that if the species had spores larger than 35 μm , then dioicism may create a serious reduction in its long-distance dispersal ability. They reasoned that for small spores there were better chances for transport by air currents, hence providing a greater chance for dioicous species with small spores to arrive near a partner of the opposite sex. To achieve the same opportunity for a partnership in species with larger spores would take a longer time. It is also important to recognize that the only dioicous species to achieve transoceanic dispersal in the Jubulaceae was *Frullania ericoides* (Figure 163), a species that is also the only one with gemmae. On the other hand, all the species in Lejeuneaceae that have gemmae are endemic.



Figure 161. *Cheilolejeunea trifaria* (Lejeuneaceae) from the Neotropics. Note the perianths, with a prominent one in the middle of the image. Photo by Michael Lüth, with permission.



Figure 162. *Cololejeunea cardiocarpa* (Lejeuneaceae) archegonia (**left**) and antheridia (**right**). Photo by Paul Davison, with permission.



Figure 163. *Frullania ericoides*, the only transoceanic member of **Jubulaceae** among neotropical liverworts, and the only member of **Jubulaceae** with gemmae there. Photo by Paul Davison, with permission.

Ecological Adaptations

Not surprisingly, van Zanten and Gradstein (1988) found a positive correlation between Neotropical liverwort species range and xerophytic habitat. They found that correlation mainly related to large spore size. There was no similar relationship for species with small spores. Moreover, they found no relationship between spore drought tolerance and moisture level of the habitat. However, for sporelings there is a significant correlation with the average number of days for survival of desiccation, with 30 days for xerophytes, 25 for mesophytes, and 13 for hygrophytes. This suggestion that successful establishment may be more important than dispersal has appeared in other studies discussed herein.

Van Zanten and Gradstein (1988; Gradstein 2013) found that tropical lowlands have significantly more transoceanic species than at higher elevations. Most of these transoceanic species are members of the Lejeuneaceae and Jubulaceae, families with large, green spores. This requires some explanation since it is easier to get higher elevation species into the airstream, and large green spores suggest a need for immediate germination. But the lowland species are generally more widespread than are montane and alpine species, providing greater availability of these lowland species. Furthermore, this widespread habitat availability is in effect at the receiving end as well, creating greater opportunity for a "stepping

stone" effect in regions where there are oceanic islands with large areas of relatively low elevation.

Who Is Travelling?

We seem to have a reasonable understanding of the algae that we are likely to encounter in diaspore rain, with genera like *Chlamydomonas* and *Chlorella* likely to show up in that translucent glass jar in which you are starting to root a plant. In fact, the water in most such glass jars will turn green before the plant has enough roots to put it in soil due to the arrival and successful colonization of *Chlorella*. But I was surprised to find we scarcely have similar information for bryophytes.

Ross-Davis and Frego (2004) examined the propagule rain in southeastern New Brunswick, Canada, forests that were managed for timber production. Using emergence, they identified 51 species in the aerial rain and soil propagule banks. Only 36 of these were extant species in the area sampled. The air-borne species were more similar to the extant vegetation than were the buried taxa, attesting to the readiness of the diaspore bank for changes in the conditions.

Anyone who has watched a disturbed area, peered at the cracks in the sidewalk, or investigated an area after a fire knows that one of the first bryophytes to arrive is often *Funaria hygrometrica* (Figure 164). To add to this list of habitats, this was the first moss to arrive and become established on the volcano Surtsey when it arose from the sea off the coast of Iceland (Schwabe 1974). This moss seemed to benefit from having its protonemata colonized by nitrogen-fixing Cyanobacteria, particularly members of the group *Schizothrix* (Figure 165)/*Plectonema* and members of the **Nostocaceae**, particularly *Anabaena* (Figure 166).

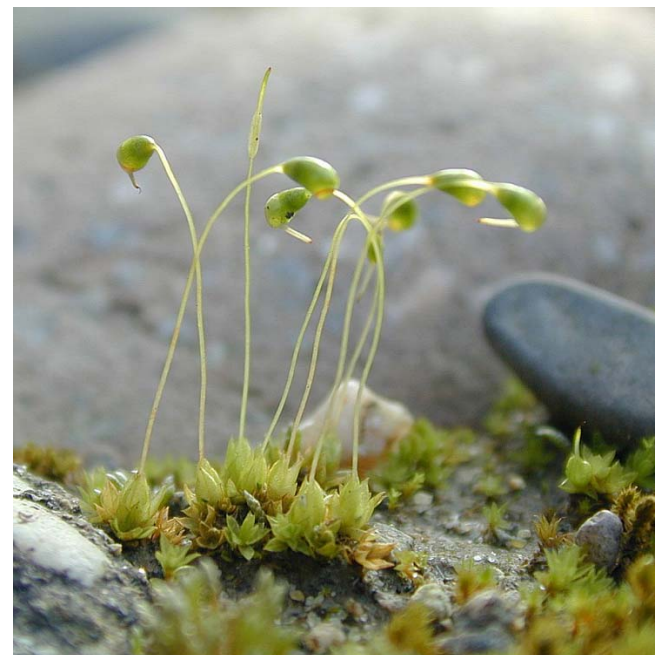


Figure 164. *Funaria hygrometrica* on rocky substrate in southern Europe. Photo by Michael Lüth, with permission.



Figure 165. *Schizothrix lenormandiana*. Photo from Cyanosite as freeware.



Figure 166. *Anabaena* sp., a common symbiont with some bryophytes. Photo by Janice Glime.

One test of the dispersal ability of bryophytes is to compare the spore rain with the extant species in the area. This will indicate those that are able to disperse there, but are unable to become established. This can be further tested by culturing the propagules to see if germination might be successful if different, and hopefully more appropriate, conditions are provided.

Certainly some species are more common in the diaspore rain than others. Leitao *et al.* (1996) and Santos *et al.* (1996) used agar traps to identify cryptogamic organisms from the atmosphere in Coimbra, Portugal. These included many non-bryophytes, but 75% of those collected were spores <25 μm (Santos *et al.* 1996). In addition to non-bryophytes [Cyanobacteria, Chromophyta (Ochrophyta), Chlorophyta, and Pteridophyta], Santos and coworkers isolated the liverworts *Fossombronia angulosa* (Figure 167-Figure 169) and *Pellia epiphylla* (Figure 170) and the mosses *Leptodictyum riparium* (Figure 171), *Bryum dunense* (Figure 172), *Ditrichum* sp. (Figure 173), *Gymnostomum aeruginosum* (= *G. calcareum*; Figure 174), *Pottia* sp. (Figure 175), and *Trichostomum brachydontium* (Figure 176). *Bryum dunense* forms axillary bulbils and *Leptodictyum riparium* is monoicous and produces abundant capsules.



Figure 167. *Fossombronia angulosa* with capsule, a species of liverwort found in agar traps. Photo by Des Callaghan, with permission.

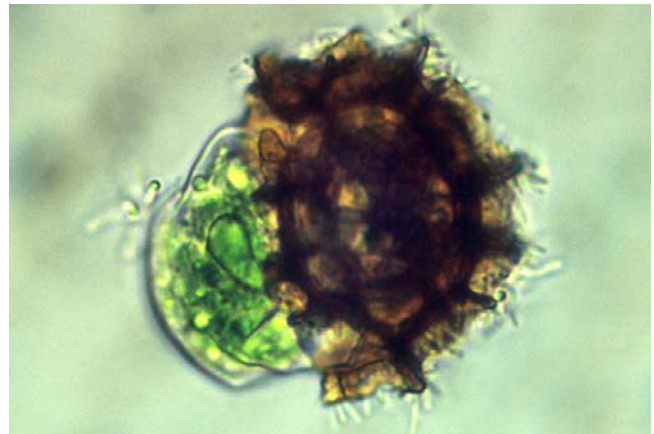


Figure 168. *Fossombronia angulosa* spore germination. Photo by Eugenia Ron and Tom Sobota, Plant Actions, with permission.



Figure 169. *Fossombronia angulosa* protonema. Photo by Eugenia Ron and Tom Sobota, Plant Actions, with permission.



Figure 170. *Pellia epiphylla* with sporophytes. Photo by Hermann Schachner, through Wikimedia Commons.



Figure 173. *Ditrichum pallidum* with capsules. Photo by Li Zhang, with permission.



Figure 171. *Leptodictyum riparium* with capsules. Photo by Michael Lüth, with permission.



Figure 174. *Gymnostomum aeruginosum* with capsules, a species found in the diaspore rain in Portugal. Photo by Hermann Schachner, through Wikipedia Commons.



Figure 172. *Bryum dunense*, one of the mosses distributing airborne propagules trapped in Coimbra, Portugal. Photo by Jan-Peter Frahm, with permission.



Figure 175. *Tortula modica* (= *Pottia intermedia*) in Europe. Photo by Michael Lüth, with permission.

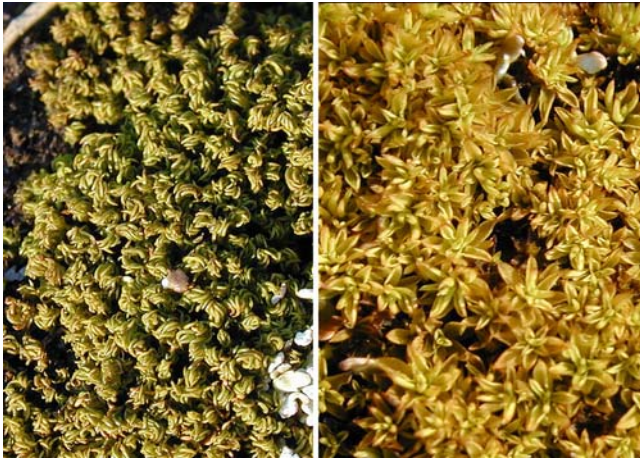


Figure 176. *Trichostomum brachydontium* showing dry (left) and wet (right). Photos by Michael Lüth, with permission.

Gaur and Kala (1984) tested what is in the spore rain compared to what is growing in the Himalayan alpine zone of India. They used adhesive-coated slides at 3600 m asl and identified spores of *Marchantia* (Figure 103), *Conocephalum* (Figure 177), *Pellia* (Figure 170), and *Metzgeria* (Figure 178) among the predominately fungal spores (65.5%) and flower pollen (23.9%). The liverworts in the spore rain were characteristic of the species growing in the area, so local dispersal could not be ruled out.



Figure 177. *Conocephalum conicum* with archegoniophores. Photo by Janice Glime.



Figure 178. *Metzgeria decipiens* spores and elaters. Photo by Tom Thekathiyil at Blue Tier, with permission.

The most comprehensive study seems to be that of Ross-Davis and Frego (2004; Table 1). They examined the propagule sources of forest floor bryophytes in two mature mixed-wood forests in southeastern New Brunswick, Canada. The bryophyte communities in the two forest locations they studied revealed 36 bryophyte taxa. They found 51 taxa in the diaspore rain and diaspore bank. They furthermore found seasonal differences in the diaspore rain. Of the extant species present, 36% were absent in both the spore rain and the diaspore bank. Both communities were dominated by the feather mosses *Pleurozium schreberi* (Figure 179) and *Hylocomium splendens* (Figure 180), and these two species were present in both the spore rain and the buried diaspore bank. But the dominant taxon in the diaspore bank was *Sphagnum* (Figure 181), which was not present among the extant flora in either location. Up to 22 species from the diaspore bank were able to germinate after a six-hour culture. The aerial diaspore composition was 62% similar between the two locations, whereas the diaspore bank had only 34% similarity.



Figure 179. *Pleurozium schreberi*, a species that appears in both diaspore banks and diaspore rain. Photo by Janice Glime.



Figure 180. *Hylocomium splendens* in autumn. Petr Brož, through Creative Commons.



Figure 181. *Sphagnum* protonemata and young plant. Photo by Andras Keszei, with permission.

Table 1. Bryophytes found in diaspore banks and aerial banks in southeastern New Brunswick, Canada. Diaspores were collected in two locations in mixed forest. Species that were in at least one of the diaspore samples at both locations are in **bold**. **DB** indicates buried diaspore bank. **DR** indicates aerial diaspore rain. Based on Ross-Davis & Frego 2004.

<i>Amblystegium serpens</i>	DB	DR	<i>Herzogiella striatella</i>	DR
<i>Atrichum crispum</i>	DB	DR	<i>Hypnum imponens</i>	DR
<i>Atrichum</i> spp.		DR	<i>Hypnum pallescens</i>	DR
<i>Aulacomnium palustre</i>		DR	<i>Hypnum</i> spp.	DR
<i>Bazzania trilobata</i>	DB	DR	<i>Isopterygiopsis pulchella</i>	DR
<i>Blepharostoma trichophyllum</i>	DB		<i>Leptobryum pyriforme</i>	DB
<i>Brachythecium reflexum</i>	DB		<i>Leptodictyum riparium</i>	DR
<i>Brachythecium starkii</i>	DB	DR	<i>Marchantia polymorpha</i>	DB
<i>Brachythecium</i> spp.		DR	<i>Mnium stellare</i>	DB
<i>Bryum pallescens</i>		DR	<i>Nowellia curvifolia</i>	DR
<i>Callicladium haldanianum</i>	DB	DR	<i>Philonotis fontana</i>	DB
<i>Campylium hispidulum</i>	DB	DR	<i>Platydictya subtilis</i>	DR
<i>Campylium stellatum</i>	DB	DR	<i>Platygyrium repens</i>	DR
<i>Cephalozia lunulifolia</i>	DB		<i>Pleuroidium subulatum</i>	DR
<i>Cephalozia</i> spp.	DB	DR	<i>Pleurozium schreberi</i>	DB
<i>Cephaloziella</i> spp.		DR	<i>Pohlia</i> spp.	DB
<i>Ceratodon purpureus</i>	DB	DR	<i>Polytrichum commune</i>	DB
<i>Chiloscyphus profundus</i> (= <i>Lophocolea heterophylla</i>)		DR	<i>Polytrichum</i> spp.	DR
<i>Dicranella rufescens</i>	DB		<i>Pseudobryum cinclidioides</i>	DB
<i>Dicranum polysetum</i>	DB		<i>Ptilidium pulcherrimum</i>	DB
<i>Dicranum scoparium</i>	DB	DR	<i>Sanionia uncinata</i>	DR
<i>Ditrichum flexicaule</i>	DB		<i>Sphagnum</i> spp.	DB
<i>Frullania oakesiana</i>		DR	<i>Syzygiella</i> (= <i>Jamesoniella</i>)	
<i>Funaria hygrometrica</i>		DR	<i>autumnalis</i>	DR
<i>Geocalyx graveolens</i>	DB	DR	<i>Thuidium delicatulum</i>	DR

But these studies are very local and tell us little about what species are most likely to be encountered in the atmosphere. There are certainly not enough studies to assess the types of characters that seem to contribute to their presence. May I suggest, then, that the most likely entrants into the aerial realm are those diaspores (mostly spores) that are small, light weight, perhaps have surface waxes or papillae that increase their surface area and buoyancy without adding proportional weight, and have some means of getting away from the capsule and into the air stream, such as the explosive expulsion of spores from a *Sphagnum* capsule (see Chapter 4-9). Research by Sundberg (2012) on *Sphagnum*, discussed in Chapter 4-8 under Everything is Everywhere, supports my last suggestion, but I have little support to offer for my other suggestions. They must also have a means to survive desiccation and protection against UV radiation. Testing these should provide for an interesting set of experiments. But first, we must find out what is in the spore rain around the world. This will be challenging because the concentrations are quite low. For example, Lewis Smith (1991) found no exotic bryophyte spores in the Antarctic air space, yet new volcanic land that was heated became colonized by species not known for more than 1000 km, suggesting that the diaspores are there in the diaspore rain but are too dilute to be sufficiently captured by our sampling methods.

Spore Dispersal Mechanisms

We might think of spore dispersal as having the same potential mechanisms as pollen dispersal, but some caveats exist. The flowers have carried the variety of dispersal

agents to extremes, utilizing birds, bats, a variety of insects, water, gravity, and wind, and to a lesser extent, other mammals and invertebrate animals. To accomplish this great diversity, especially among the animal vectors, the flowers have spent tremendous energy in the production of attracting organs (the flowers themselves) that have colors, shapes, odors, and rewards that beguile their benefactors. Among the bryophytes, such extravagant expenditures of costly energy and biomass are rare, but some do exist (see subchapter 4-8).

For the seed plants, Hughes *et al.* (1994) concluded that plant growth form and stature can exclude certain dispersal modes. Since bryophytes generally are shorter in stature than their tracheophyte counterparts, we could expect all of them to exclude certain types of dispersal such as being eaten by large mammals. But some bryophytes could get around this problem by growing on trees, should any be suitable food for tall mammals. Their growth forms are such that they easily trap spores that pass by them, so the elevation of the capsule on a seta in most species seems necessary to reduce self-entrapment.

The third conclusion of Hughes *et al.* (1994) was that the availability of specific dispersal vectors seems to have no influence on dispersal mode. That conclusion needs some consideration, and dispersal vectors will be discussed in a later subchapter. But the wide range of dispersal vectors available to seed plants seems to have little similarity to the dispersal modes used by or even available to bryophytes in the same habitats, largely due to the small size of both the bryophyte plants and the propagules (Hughes *et al.* 1994).

Finally, Hughes *et al.* (1994) concluded that attributes of the physical environment rarely are important except indirectly through influencing plant stature and seed size. We have discussed above the meager evidence to support the influence of the physical environment on spore size in bryophytes; for example, it does seem that ephemeral habitats may have placed a selection pressure for larger spores [e.g. Bijlsma *et al.* 2012 for *Ephemerum* spp. (Figure 98)]. Living among other vegetation that can trap the spores, including forest canopies, may prevent them from getting into the air stream. I do wonder if bryophytes that live high on vertical surfaces (Figure 182) may be influenced in their success by the greater opportunity for wind carriage due to greater wind velocity, as shown for seeds by Greene and Johnson (1996). Perhaps there is a relationship to spore size and in some cases to the plant overall structure in such habitats.



Figure 182. *Tortella fragilis* at Khibiny Mountains, Apatity, Murmansk, demonstrating a vertical substrate at a high elevation where it might more easily become windborne. Photo by Michael Lüth, with permission.

Sporophyte Adaptations for Dispersal

Hedenäs (2001) elevated the role of dispersal in evolution and considered spore dispersal to be one of the two functions causing differences in character state frequencies among various environments. He considered such spore dispersal to be related to **shape** and **orientation of capsules**, **annulus**, **appearance of exostome** and **endostome**, **spore size**, **spore maturation time**, and **seta length**. One might ask if aquatic mosses in general have short or absent setae, as in *Fontinalis* (Figure 144), thus reducing the chance of drag dislodging the capsule before maturity, and do epiphytes truly more commonly have erect capsules?

Stark (2001) compared capsule adaptations of two Mojave Desert species of mosses. They differed both in morphology and in period of distribution. The *Grimmia orbicularis* capsule (Figure 183) is inclined, short, and broad, releasing its spores over about 6 months; its position on nearly vertical rock surfaces permits it to drop the opercula and liberate spores quickly. The ground-dwelling *Syntrichia inermis* (Figure 184) releases its spores from a single cohort of capsules over a period of three years. Dispersal of the operculum and spores is less certain for this soil-dwelling species, and the operculum detachment period can last up to 2.5 years.



Figure 183. *Grimmia orbicularis* from southern Europe, showing the short, broad, inclined capsule and the vertical substrate. Photo by Michael Lüth, with permission.



Figure 184. *Syntrichia inermis* growing on soil. Photo by Jan-Peter Frahm, with permission.

Crawford *et al.* (2009) found an evolutionary relationship between separate sexes and small spores, although this might be backwards since it appears that evolution in mosses tends to go from the dioicous condition to the monoicous one through doubling of the chromosome number (often through the failure of meiosis) or addition of a sex chromosome. Hence, we might consider that large spores are more common in monoicous taxa, a phenomenon that might result from the doubling of chromosome number.

Most bryophyte spores are wind dispersed, carrying many, probably most, to unsuitable habitats, but usually assuring that at least some will not land among their parents. Nevertheless, some bryophytes have evolved ingenious dispersal mechanisms. The simple bryophytes lack the resources to create such large and elaborate structures as flowers, but have, even so, in some cases (e.g. *Splachnaceae*, Figure 185) created highly visible and odiferous attractions to their dispersal vectors, as described in Chapter 4-9 of this volume. Nevertheless, most bryophytes seem to rely on wind and gravity as their primary dispersal agents. To this end, **mosses** have developed elaborate **peristome** teeth (Figure 186) that move in response to moisture changes and that tend to facilitate spore dispersal in dry air when the greatest opportunity for wind dispersal prevails (Bonnot 1978). The teeth are covered by an **operculum** (Figure 187) that seals the capsule and that is usually shed in response to drying and shrinkage of the capsule. It appears that this mode is highly successful, and the exceptions to wind dispersal are few.



Figure 185. *Splachnum rubrum* capsules displaying their showy hypophysis that attracts flies. Photo by Michael Lüth, with permission.



Figure 186. *Brachythecium velutinum* capsules showing double peristome. Photo by Dick Haaksma, with permission.



Figure 187. *Brachythecium populeum* capsules showing opercula. Photo by Des Callaghan, with permission.

One of the features of sporophytes that has fascinated my students is the twisting of the seta. When a dehydrated moss with sporophyte intact is hydrated, the seta of many species, e.g. *Dicranella heteromalla* (Figure 188), will gyrate in a spiral fashion, loosely coiling and uncoiling as its cells become hydrated, presumably unequally. Unfortunately, I have not observed that this has any effect on spore dispersal and must wonder if it is simply a consequence of the anatomy with no adaptive consequence at all. I am constantly reminded by the bryophytes that "all life has a twist in it."



Figure 188. *Dicranella heteromalla* with capsules and twisted setae that gyrate when the moisture changes. Photo by Biopix, through Creative Commons.

Sundberg (2005) examined capsule size in *Sphagnum* (Figure 189) to determine its possible role in dispersal distance. He tested four species of *Sphagnum* and found that the diameter of the capsule containing the spores was negatively correlated with the proportion of spores remaining in the capsule after dehiscence (5-16%), negatively correlated with those being deposited within the colony (2-14%), and negatively correlated with those being deposited between the colony edge and the outer sampled perimeter of 3.2 m (7-22%). These negative correlations imply that the larger diameter of the capsule somehow facilitates a greater dispersal distance.



Figure 189. *Sphagnum fimbriatum* with capsules that have lost their opercula. Photo by David T. Holyoak, with permission.

Thiers (1988) described morphological adaptations of the dispersal of liverwort propagules in the order *Jungermanniales* to their tropical habitat. These included precociously germinating spores (spores that germinate within the capsule; Figure 190-Figure 191), followed by a prolonged protonemal stage, and culminating in a **neotonic** life cycle (reproducing at an early developmental stage).

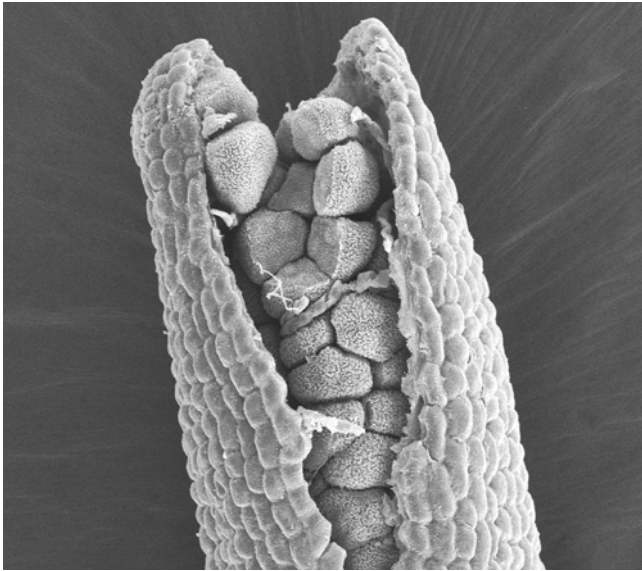


Figure 190. *Dendroceros* multicellular spores in capsule. Photo courtesy of Karen Renzaglia.

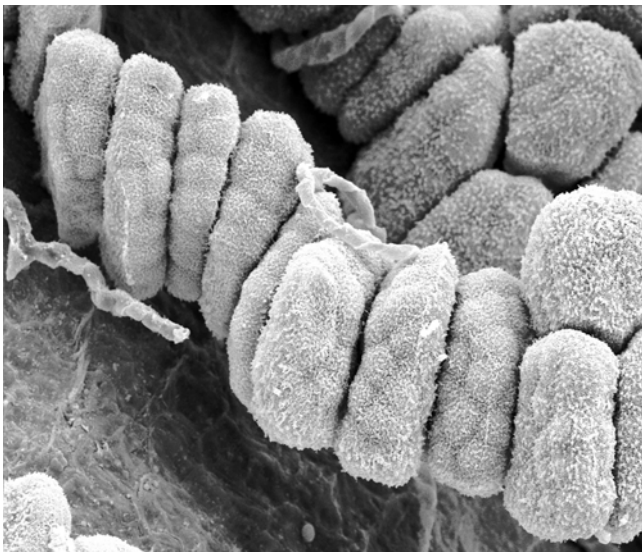


Figure 191. *Dendroceros* sp. (Anthocerotophyta) with stacks of multicellular spores, showing **precocious germination**. Photo courtesy of Karen Renzaglia.

Role of Peristome

The peristome teeth have various patterns of movement, with some resting inward and others resting outward. The structure of the teeth often causes uneven shrinkage as they dry, causing them to pulsate or even twist. Patterson (1953) described three behavior types for peristome teeth:

1. teeth wherein outer teeth either exclusively or predominately bend inward [*Ceratodon* (Figure 192), *Barbula* (Figure 193), *Pylaisia s.l.* (Figure 194)]
2. teeth with outer teeth shrinking exclusively or predominately bending outward [*Grimmia* (Figure 195), *Orthotrichum* (Figure 196-Figure 197), *Dicranum* (Figure 198)]
3. teeth that oscillate strongly as they change from shrunken to swollen states [*Amblystegium* (Figure 199), *Hypnum* (Figure 200), *Neckera* (Figure 201), *Bryum* (Figure 202)]



Figure 192. *Ceratodon purpureus* peristome, where teeth mostly bend inward. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

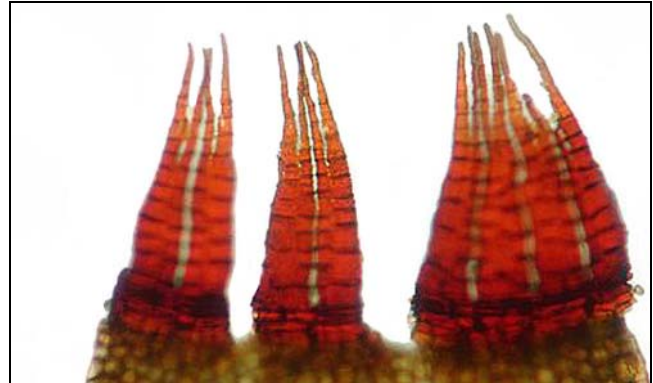


Figure 193. *Barbula amplexifolia* peristome from India, a species whose teeth bend inward. Photo by Michael Lüth, with permission.



Figure 194. *Pylaisiella polyantha* sporophytes showing teeth bending inward. Photo by Des Callaghan, with permission.



Figure 195. *Grimmia ungeri* with capsules showing outward-pointing teeth. Photo by Michael Lüth, with permission.



Figure 196. *Orthotrichum diaphanum* with capsules showing reflexed (outward-bending) teeth. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

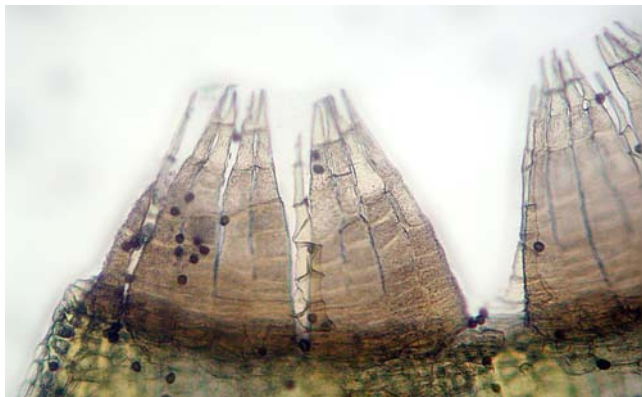


Figure 197. *Orthotrichum alpestre* peristome. Photo by Michael Lüth, with permission.

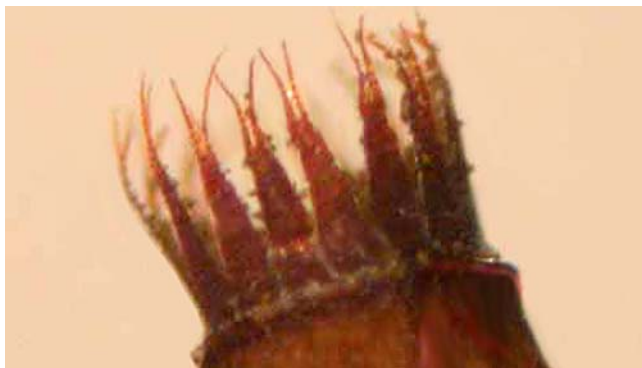


Figure 198. *Dicranum scoparium* peristome with teeth that bend outward upon drying. Photo from UBC botany website, with permission.



Figure 199. *Amblystegium subtile* with capsules showing teeth that flex as they change moisture states. Photo by Hermann Schachner, through Creative Commons.



Figure 200. *Hypnum cupressiforme* capsule showing peristome with teeth that flex as they change moisture states. Photo by Malcolm Storey, through Creative Commons on Discover Life.



Figure 201. *Neckera pennata* branch with capsule and teeth that oscillate in response to moisture changes. Photo by Dale A. Zimmerman, Herbarium, Western New Mexico University, with permission.

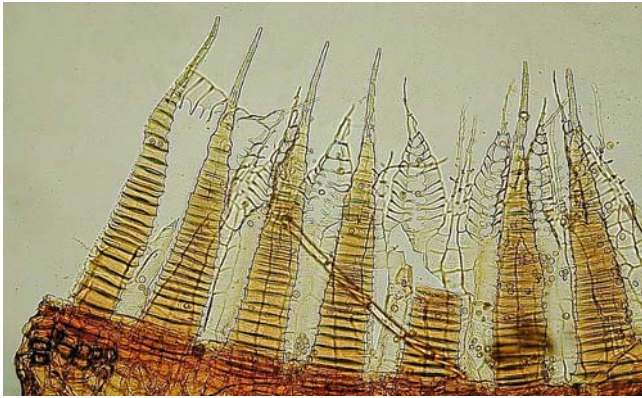


Figure 202. *Bryum caespitium* peristome, with teeth that flex as they change moisture states. Photo by Michael Lüth, with permission.

Schnepf *et al.* (1978) described the movement of the outer peristome in the moss *Racomitrium intermedium* (Figure 203). This movement arises from different swelling velocities of the outer plates and inner ridges of wall thickenings. These swelling differences arise from the suberin-like substances and wax lamellae enclosing the ridges. There is no suberin-like material in the plates.



Figure 203. *Racomitrium intermedium* with capsules. Photo by Michael Lüth, with permission.

Estébanez *et al.* (2002) determined that strongly bound lipids, phenolics, and non-cellulosic polysaccharides were responsible for the movement of the teeth in *Arctoa fulvella* (Figure 204), *Grimmia decipiens* (Figure 205), *Grimmia pulvinata* (Figure 206), *Schistidium rivulare* (Figure 207), *Bucklandiella sudetica* (= *Racomitrium sudeticum*; Figure 208), *Ptychomitrium sinense* (Figure 209), *Glyphomitrium humillimum* (Figure 210), and *Venturiella sinensis* (Figure 211).



Figure 204. *Arctoa fulvella* with capsules. Photo by Andrew Hodgson, with permission.

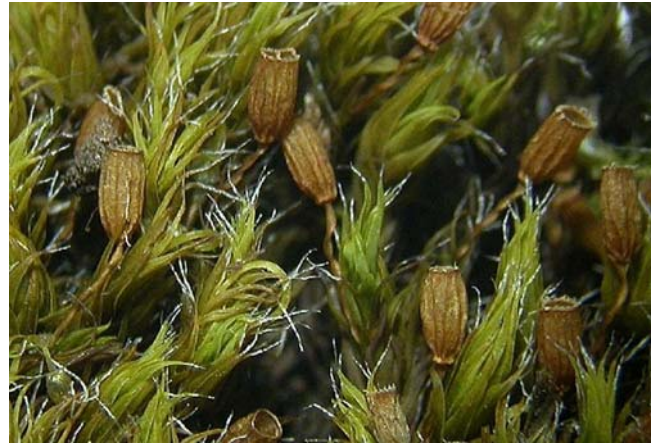


Figure 205. *Grimmia decipiens* with capsules. Photo by Henk C. Greven, Doorn, The Netherlands, with permission.



Figure 206. *Grimmia pulvinata* with capsules and teeth pointing outward. Photo by Michael Lüth, with permission.



Figure 207. *Schistidium rivulare* with capsule showing outward-pointing teeth and operculum attached by columella. Photo courtesy of Betsy St. Pierre.



Figure 208. *Bucklandiella sudetica* showing reflexed peristome teeth. Photo by Hermann Schachner, through Creative Commons.



Figure 209. *Ptychomitrium sinense* in dry state. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.



Figure 210. *Glyphomitrium humillimum* with capsules. Photo by Okayama Prefectural Nature Conservation Center, permission pending.



Figure 211. *Venturiella sinensis* with capsules. Photo from Hiroshima University, with permission.

Takakia ceratophylla (Figure 212) has a dispersal mechanism that is unusual among mosses. The capsule has a spiral line of dehiscence. At maturity, when the capsule splits, this suture causes a spiral twisting that seems to help in spore dispersal (Higuchi & Zhang 1998). In many of the mosses, the annulus becomes modified as the capsule dries. For example, in *Ludorughya springbokorum* the annulus rolls inwards, nearly covering the opening of the capsule (Hedderston & Zander 2007). Upon wetting, it rapidly everts, expanding the capsule opening. This exposes the two-sized spores within.



Figure 212. *Takakia ceratophylla* capsule showing spiral split. Photo by Ken McFarland, with permission.

Some bryophytes do not typically shed the operculum, but instead rely on disintegration of the capsule wall. *Buxbaumia aphylla* (Figure 213) seems rarely to shed the operculum (Glime & Liao, pers. obs.). Instead, the capsule cracks across its broad, flat upper face, peeling back to expose the spores (Figure 213). Eventually the tissue peels away, permitting the spores to escape. The protonema in this species produces sporophytes every year, and in Newfoundland, these sporophytes, which must overwinter to release the ripe spores in spring, can suffer high mortality from sudden frosts (Hancock 1973). *Diphyscium* (Figure 214) has a capsule with a similar small opening, but it does seem at least to shed the operculum. If it relies on the capsule splitting, I have not yet been able to observe it.



Figure 213. Capsules of *Buxbaumia aphylla* showing peeled away capsule wall on upper capsule. Photo by Janice Glime.



Figure 214. *Diphyscium foliosum* females with capsules showing shed operculum and teeth. Photo by Michael Lüth, with permission.

From my own observations, I concluded that *Fontinalis* (Figure 144) depends on abrasion for loss of the operculum. In spite of its beautiful lattice teeth, the operculum remains intact and winter-borne capsules become abraded by the silt load of melt waters. This abrasion removes sufficient tissue for spore dispersal to occur. In the absence of abrasion, the capsules seem to be so impregnated with phenolic compounds that the suture between the operculum and capsule body firmly glues them

together. But others have observed the beautiful teeth and spore dispersal, so my observations may only be of the unsuccessful capsules that remained after the others had dispersed their spores.

Cleistocarpy

In some mosses, the capsules have no peristome or operculum, a condition known as **cleistocarpy**. Such is the case for *Archidium ohioense* (Figure 109) and *Trachycarpidium tisserantii* (Makinde & Odu 1994). As already noted, these two species had poor spore release, compared to that of the two peristomate mosses, *Fissidens ovatifolius* (as *Fissidens minutulus*; Figure 215) and *Bryum coronatum* (Figure 93). All four species benefitted in their savannah habitat in Nigeria by having a rapid maturation cycle for their capsules.



Figure 215. *Fissidens ovatifolius*. Photo by Jan-Peter Frahm, with permission.

In *Archidium* (Figure 109), the cleistocarpous capsule hides on a short seta among the leaves. At maturity, the capsule wall ruptures by decomposition, permitting spores to escape (Lönnell 2011). Lönnell suggests that this method of spore exposure and the large size of the spores are not supportive of wind dispersal and that use of another agent, perhaps water, is more likely. *Riccia* species likewise have large spores (Figure 216). Their presence in flood plains and other habitats that periodically get reasonably inundated with running water suggests that the same may be true for them.

Herrnstadt and Heyn (1988) have pointed out to us that a similar elaborate, complex, **sexine** (outer, sculptured layer of exine) spore wall pattern is common to a large percentage of the species that have cleistocarpous capsules or lack a peristome. These cleistocarpous species typically are small mosses, annual, terrestrial, and living in open habitats, particularly in the Mediterranean and adjacent arid regions. They furthermore have capsules that are immersed in the perichaetial leaves and possess large spores [(25) 30-40 μm]. Does this mean that this spore wall pattern has an adaptive value in arid regions?



Figure 216. *Riccia sorocarpa* showing the large, highly pigmented spores. Photo by Des Callaghan, with permission.

Summary

Diaspores include both spores and other propagules that serve in dispersal. These are typically sampled by exposed agar plates, glass slides with glycerine, or traps, including Tauber and Burkard traps.

Spores are usually smaller than vegetative diaspores and are therefore the most successful agents of long-distance dispersal in bryophytes, whereas vegetative means help the population to become established and spread once having arrived. But spores require fertilization as a prerequisite and therefore nearness of males and females. Vegetative diaspores continue in production under stressful conditions, but spores do not. Fragmentation is common in many species and seems only to require dry conditions; animals can help both in fragmenting and in carrying these propagules.

The success of dispersal and range size seems to be related to the abundance of sporophyte production. On the other hand, genetic information, at least for some species (especially **Polytrichaceae**), suggests that vegetative dispersal may be more important, even in species that produce abundant spores, perhaps due to spore dispersal limitations.

Dispersal success requires a tradeoff between energy spent on short-distance but energy-rich diaspores and energy wasted for a few of many spores produced that succeed in long-distance dispersal. Vegetative reproduction requires a tradeoff between likely success and loss of genetic diversity. Liverworts, as a group, seem to spend more energy on asexual reproduction than do mosses.

Disturbance can create conditions for vegetative growth, bring buried diaspores to the surface where they can germinate, and disperse propagules for short or long distances. Some species are especially adapted to

disturbances such as fires, floods, cold events, and even ants.

Diaspore banks are important for species that live in disturbed habitats. The spores of species that are regularly disturbed, such as floodplains, are typically large and these species may have rhizoidal tubers or other forms of rhizoidal propagules. For those that grow in areas of unpredictable disturbances, taxa that are easily dispersed, such as *Funaria hygrometrica* and *Marchantia polymorpha*, are often important colonizers and can survive in spore banks as well as arriving through aerial dispersal. Representation in the diaspore banks often does not reflect the species at the surface, but rather has a strong bias toward acrocarpous species and species of early successional stages.

Peristome teeth in mosses, an **explosive capsule** in *Sphagnum*, and **claters** in liverworts help in dislodging spores and dispersing them. Other factors influencing dispersal are capsule size, shape, and orientation, annulus, exostome, endostome, spore size, maturation time, and seta length. Some rely on splitting of the capsule, including **cleistocarp**. Strongly bound lipids, phenolics, and non-cellulosic polysaccharides contribute to peristome movement. Flood plain species tend to have large spores that permit a rapid life cycle. Dioicous species tend to have smaller spores, permitting them to travel farther on those occasions when sexual reproduction is successful. In some species, the spore size varies with altitude.

Maturation time can be important. For most spores, a dry atmosphere is favorable for longer distance dispersal. For vegetative propagules, some are favored by rain and others by dry wind.

It is likely that many species have spores that can survive years of dormancy, and some may survive hundreds of years while dry and in the dark. Those that start to germinate, then dry out again, will most likely die. Spores are also kept dormant by their parents, most likely due to chemicals from the parents.

Acknowledgments

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CHAPTER 4-8

ADAPTIVE STRATEGIES: TRAVELLING THE DISTANCE TO SUCCESS

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CHAPTER 4-8

ADAPTIVE STRATEGIES: TRAVELLING THE DISTANCE TO SUCCESS



Figure 1. *Conostomum tetragonum* with capsules in the mountains of Norway where its spores become windborne more easily than those of bryophytes in the forest. Photo by Michael Lüth, with permission.

Diaspore Travel Distances

Although bryophyte spores are typically wind-dispersed, it appears that few actually travel very far. Most never actually become airborne (Wyatt 1977; Stoneburner *et al.* 1992). More typically, most of the spores fall within a meter or less (Crum 2001) of the capsule. It is likely that the bryophytes themselves act as spore traps, particularly for the neighboring plants of their own species. Pardoe *et al.* (2010), using mosses to compare trapping efficiencies, demonstrated that mosses serve as traps for pollen, suggesting that they should be traps for bryophyte spores as well.

But trapping spores and quantifying atmospheric spore rain is difficult at best, and the worldwide distribution of a number of taxa attests to the fact that these diaspores must at least occasionally travel great distances. There are tests of survivability for spores, but even less is known about vegetative diaspores.

Failure to Leave Home

Most spores will fall near the parent. In *Tortula truncata* (= *Pottia truncata*; Figure 2), 67% of the spores released fell within the parent clump and 70% within 2 m (Roads & Longton 2003). Further evidence of lack of gene flow to new locations is that there was little or no genetic variation within the individual clumps, but no genotypes were in common between the populations, suggesting that genes (including those in spores) from one population clump had not reached the other one. Sundberg (2005) found that for six species of *Sphagnum* (Figure 3), 8–32% of the spores that dispersed beyond the colony did not travel beyond the active release area of 3.2 m. Stoneburner *et al.* (1992) demonstrated this stay-at-home behavior experimentally for *Atrichum angustatum* (Figure 5). In that species, 94% of the spores were collected within 2 m of the colony center; 1% were found 15 m from the center. On the other hand, Miles and Longton (1990, 1992b) found

that more than 80% of the spores of *Atrichum undulatum* (Figure 6) and *Bryum argenteum* (Figure 7) travelled beyond their 2-m trapping distance.



Figure 2. *Tortula truncata* (= *Pottia truncata*) with capsules; most of the spores fall within the parent clump. Photo by Des Callaghan, with permission.



Figure 3. *Sphagnum fimbriatum* with capsules. Photo by David Holyoak, with permission.



Figure 4. *Tortula acaulon* (= *Phascum cuspidatum*) with capsules. Photo by Jan-Peter Frahm, with permission.

In *Tortula acaulon* (= *Phascum cuspidatum*) (Figure 4), 98% of the spores remained within the colony in this annual shuttle species (Roads & Longton 2006). This resulted in three of the five permanent quadrats having this species in them again in the second year. Many of the

second-year colonies overlapped with the position of the first-year colonies, suggesting that spores fell close to home.



Figure 5. *Atrichum angustatum* with immature capsules; most spores apparently travel more than 2 m. Photo by Janice Glime.



Figure 6. Gametophytes and sporophytes of *Atrichum undulatum*. Photo by Michael Lüth, with permission.



Figure 7. *Bryum argenteum* with capsules in Europe. Most spores are apparently able to travel more than 2 m. Michael Lüth, with permission.

Polytrichaceae

Atrichum undulatum (Figure 6) may not be a good example of dispersal distance in bryophytes due to its

presence of an epiphragm. This membrane, a characteristic of the **Polytrichaceae**, connects the 32 teeth and prevents spores from leaving from the top of the capsule, forcing them to leave between the teeth (Figure 8-Figure 9; see also Figure 56). Such a mechanism precludes the upward thrust that might be seen in some capsules where spores can travel upward directly. Rather, it is likely that spore dispersal in this species is facilitated by raindrops on the epiphragm, as is known for *Dawsonia* (Figure 10), limiting its dispersal (van Zanten 1973) both by the wet atmosphere and the horizontal ejection because they are not ejected high enough to reach the wind turbulence.

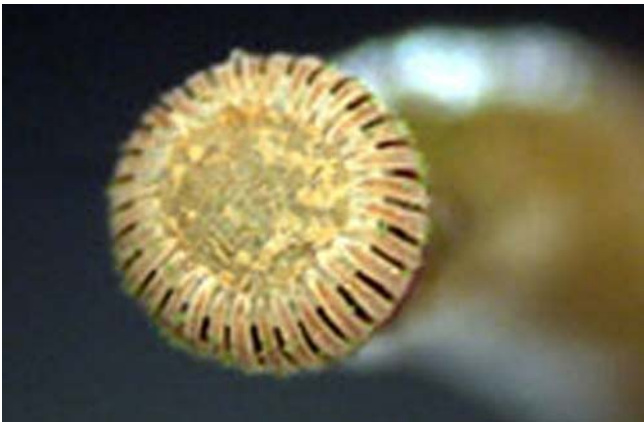


Figure 8. *Atrichum undulatum* showing epiphragm membrane extended across opening and attached to teeth like a trampoline. Photo from UBC website, with permission from Wilf Schofield.

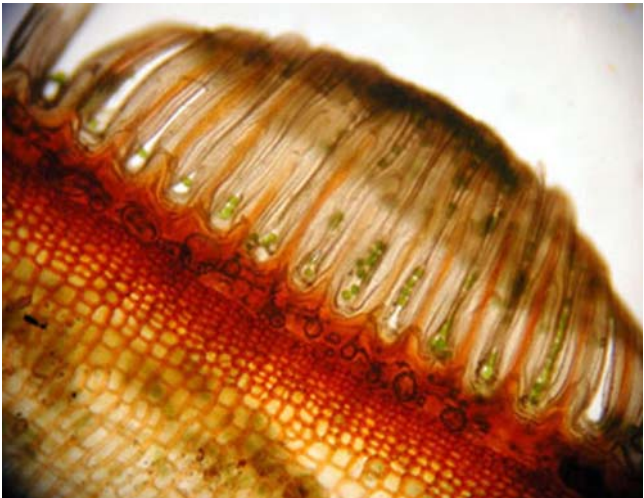


Figure 9. *Atrichum undulatum* with openings between peristome teeth showing spores. Photo from UBC website, with permission from Wilf Schofield.

Thus, based on limited data, it seems to be accepted that most bryophytes probably only disperse the majority of their spores within about 2 m (Table 1). But only a few spores need go farther to accomplish long-distance dispersal, and some species seem more able than others to accomplish this. Stoneburner *et al.* (1992) found that when air volume was increased, 4.5 million out of 25.8 million spores of *Atrichum angustatum* (Figure 5) from the colony reached the limits of their 15-m study area. Just think what would happen to spores caught in the updrafts of a forest fire or tornado!



Figure 10. *Dawsonia longiseta* with capsules. Photo by Niels Klazenga, with permission.

Table 1. Published maximum dispersal distances of bryophyte spores, based on direct measurements to traps. It is appropriate to consider that these spores will travel at least this far.

<i>Sphagnum subtile</i>	75-100 cm	McQueen 1985
<i>Tetraphis pellucida</i>	2 m	Kimmerer 1991
<i>Bryum argenteum</i>	>2 m	Miles & Longton 1992b
<i>Atrichum undulatum</i>	>2 m	Miles & Longton 1992b
<i>Tortula truncata</i>	> 2m	Roads & Longton 2003
<i>Ptilidium pulcherrimum</i>	2.5 m	Crum 2001
<i>Atrichum angustatum</i>	>15 m	Stoneburner <i>et al.</i> 1992

Evidence from a Road Cut

Miller and McDaniel (2004) used a novel method to estimate the distance and rate of dispersal that delivered new species to a new substrate. Using a highway construction site on Whiteface Mountain, New York, USA (Figure 11), they examined the bryophytes on concrete mortar there and found that it had increased the bryophyte diversity by 50% above that found on local rock substrata. The local and mortar bryophyte floras differed considerably. Many of these new species were typical of lower elevation forests, at least 5 km distant, where they were not on concrete. The new diversity suggested that these colonizers had arrived and established at the rate of at least one species per year during the 65 years since the highway construction. Miller and McDaniel concluded that for at least some bryophytes, dispersal over 5 km or more are routine events.



Figure 11. Whiteface Mountain, NY, with new-fallen snow at the summit. Photo from Wikimedia Commons.

Epiphytes

For epiphytes, dispersal must necessarily be more than a few meters for the species to survive natural die-off of forest trees, not to mention the ravages of harvesting. Snäll *et al.* (2003) found that the occurrence of the epiphyte *Orthotrichum speciosum* (Figure 12) in a fragmented forest landscape was most affected by shading, but also by connectivity to nearby tree patches, aspen (*Populus*) tree diameter, and forest vitality, suggesting that age of forest was a contributing factor, perhaps in providing more time for colonization. Furthermore, once either *O. speciosum* or *O. obtusifolium* (Figure 13-Figure 14) became established on a tree, the species remained there until the tree died. Local extinctions were entirely a function of the life of the host tree. Hedenäs *et al.* (2003) found that environmental variables seemed to have little influence on the epiphytes (including *O. obtusifolium*) in a *Populus tremula* stand. Rather, asexually dispersing species were more common than sexually dispersing ones. Sexually dispersing species tended to be more aggregated than the tree species, whereas the asexually dispersing ones had a distribution similar to that of their host.



Figure 12. *Orthotrichum speciosum* with capsules. Photo by Michael Lüth, with permission.



Figure 13. *Orthotrichum obtusifolium* on bark, a species that remains with its host tree until the tree dies. Photo by Michael Lüth, with permission.



Figure 14. *Orthotrichum obtusifolium* with gemmae on leaves. Photo by Michael Lüth, with permission.

The occurrence of *O. obtusifolium* (Figure 13-Figure 14) in the fragmented landscape was controlled by similar variables but with different relative importance. Unlike *O. speciosum* (Figure 12), colonization of *O. obtusifolium* was not affected by connectivity. Snäll *et al.* (2004a) found that there was significant kinship between individuals of both *Orthotrichum speciosum* and *O. obtusifolium* up to 350 m apart. Snäll and coworkers suggested that this indicated they were dispersal limited and might be threatened by current silvicultural practices. Nevertheless, this distance is superior to that of the species listed in Table 1, although it probably represents **stepping stone** dispersal, discussed below.

For the epiphyte *Neckera pennata* (Figure 15-Figure 16) the past history of its occurrence accounted for much of its current distribution, emphasizing the importance of nearby sources of diaspores (Snäll *et al.* 2004b). Snäll and coworkers (2004b) suggested that its dependence on connectivity, tree age, and tree diameter (a surrogate for tree age) indicate a restricted dispersal range for *Neckera pennata*. Its primary distribution at heights of less than 1.6 m on the tree could also be a response to the restricted dispersal range.



Figure 15. *Neckera pennata* on bark of *Thuja occidentalis*. Photo by Janice Glime.



Figure 16. *Neckera pennata* branch with capsules, a species that seems to be dispersal limited. Photo by Jan-Peter Frahm, with permission.

Disturbed and Short-lived Substrata

One might assume that short-lived substrata would drive selection for species that have good dispersal capability. It appears that *Ptilidium pulcherrimum* (Figure 17) from rotting logs in the coastal peninsula of northern Sweden has a somewhat better dispersal than the epiphytes mentioned above where the tree substrate is stable for a longer period of time. Söderström and Jonsson (1989) found that only 43% of the spores of log-dwelling *Ptilidium pulcherrimum* produced remained within 2.5 m of the source, suggesting that 57% were able to travel far enough to reach logs at a greater distance than that.



Figure 17. *Ptilidium pulcherrimum*, a log- and soil-dwelling species that relies on superior dispersal. Photo by Michael Lüth, with permission.

The soil-dwelling *Atrichum angustatum* (Figure 5) seems to be less adapted for dispersal than the log-dwelling *Ptilidium pulcherrimum* (Figure 17), with 94% of the spores of the former falling within 2 m of the colony center, and another 1% falling in the range of 15 m (Stoneburner *et al.* 1992). Hence, the soil-dwelling populations of *P. pulcherrimum* are prepared for dispersal to a greater distance as their habitat becomes uninhabitable. It is therefore not surprising to find it among the early colonizers of disturbed soil banks and other newly cleared soil in forests as well as on decaying logs.

Herben, *et al.* (1991), likewise using rotting logs, considered the number of spores needed to give rise to

enough new colonies that a bryophyte species could persist in this system of temporary habitat patches. To answer this question, they studied the invasive moss *Orthodontium lineare* (Figure 18) in southern Sweden. This species invades rotting wood, and based on model simulations, its success depends primarily on spore transport and establishment. Disturbance rate, competition, and colony growth are of lesser importance.



Figure 18. *Orthodontium lineare* with numerous capsules that help it to be an invasive species. Photo by David Holyoak, with permission.

If a species thrives in a periodically disturbed habitat such as an arable field or floodplain, then it needs a means of surviving and distributing to suitable substrata when favorable growing conditions occur. But the most favorable circumstances typically are those where it currently exists, and although it is likely that nearby areas are suitable, many distant areas most likely are not. Hence, such species are often adapted for rapid colonization and short-distance dispersal. With these considerations in mind, it is somewhat surprising that diaspore banks in these habitats are typically dominated by spores, such as those of *Physcomitrium sphaericum* (Figure 19; During 1997). On the other hand, habitats with small scale but somewhat regular disturbances usually have species that mostly reproduce asexually.



Figure 19. *Physcomitrium sphaericum* with capsules, a common species in diaspore banks. Photo by Li Zhang, with permission.

In peatlands, disturbances from mining are large scale and recolonization occurs on a bank of peat. The disturbance exposes deep peat where propagules have collected for centuries (Poschlod 1995). Poschlod found that some *Sphagnum* spores can germinate from these older peats following disturbance that exposes them to light. He found that the species appearing after these disturbances are typical of the original vegetation, are represented in the diaspore bank, and are often absent in the diaspore rain. This was likewise true in a dry heath, where the dominant bryophyte re-colonizer was *Campylopus pyriformis* (Figure 20-Figure 21).



Figure 20. *Campylopus pyriformis* with abundant capsules. Photo by Jan-Peter Frahm, with permission.



Figure 21. *Campylopus pyriformis* showing detached leaves that can serve as propagules. Photo by Michael Lüth, with permission.

Richards (1988) considered all substrata useful for bryophyte colonization in tropical forests to be impermanent. He therefore considered it important for those species inhabiting such substrata to have efficient short-distance dispersal. The same will be discussed below (Spore Size and Number) for *Archidium* (Figure 22) species, with large spores, cleistogamous capsules, and poor dispersal ability.

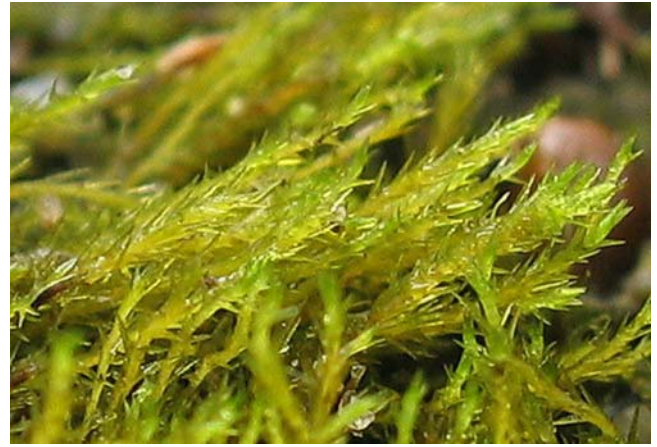


Figure 22. *Archidium alternifolium*. Photo by Andrew Spink, with permission.

Kubisch *et al.* (2014) summarized the importance of interacting factors in facilitating or preventing successful dispersal. Such factors include abiotic factors (wind, air currents) and adaptation to the new environment. They describe these as a "dynamic equilibrium of colonization and local extinction events." These principles should apply to bryophytes.

Long-Distance Dispersal (LDD)

For many bryophytes, there is at least indirect evidence that long-distance travel occurs. On Signy Island in the Antarctic, Marshall and Convey (1997) trapped spores of all five taxa of bryophytes at distances of 0.5-1 km from the nearest known sources, attesting to their ability to travel beyond a short distance. In this case, the spores were more abundant than bryophyte plant fragments in the trappings, and the representation of both was proportionately smaller than that of lichens.

A number of studies have demonstrated that typical bryophyte distance curves for spore dispersal are **leptokurtic** (Mogensen 1981). That is, they look like an exponential curve, but with a fat tail, *i.e.*, the numbers are greater close to the source and again at substantial distances than would be expected (Figure 23).

Lessons from Tracheophytes

Nekola and White (1999) took a comprehensive approach to evaluating the long-distance dispersal of bryophytes by comparing them to tracheophytes. They examined bryophytes in North American spruce-fir forests and Appalachian montane spruce-fir forests to estimate the rates of "distance decay." Predictably, the similarity of numbers compared to the source decreased significantly with distance. They found that the rate of similarity decay was 1.5-1.9 times as high for tracheophytes as for bryophytes, *i.e.*, bryophytes disperse farther. They considered that two factors cause distance decay: decrease in suitable habitat and limits to dispersal. Since the habitats were the same for both the bryophytes and the tracheophytes, it would imply that either the bryophytes have broader ecological amplitude for such factors as soil type, temperature, moisture, and day length, or they have greater dispersal ability. It is likely that both are true.

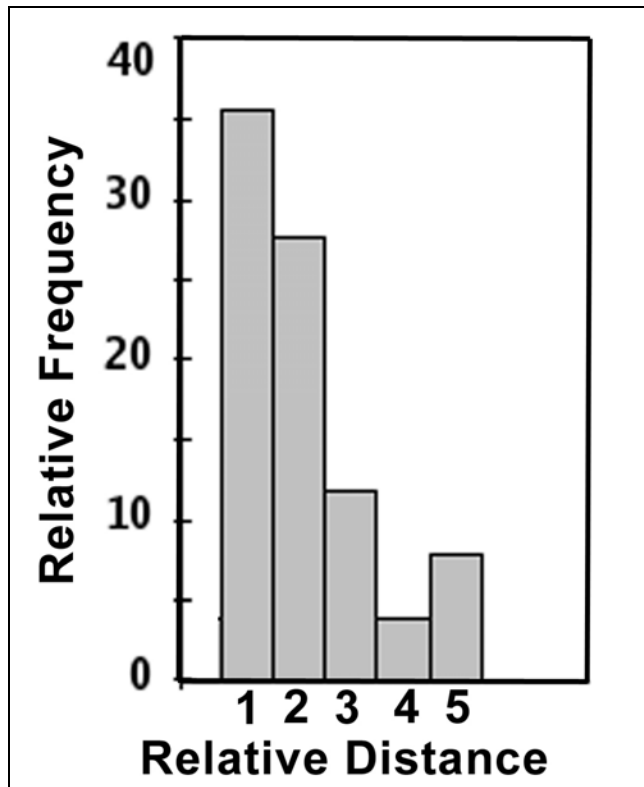


Figure 23. Hypothetical leptokurtic data graph showing asymmetrical distribution of data with a fat end on the right. Based on graph by Audrius Meskauskas through Wikimedia Commons.

Iwatsuki (1972) had a somewhat different perspective on the dispersal of bryophytes and their geographic isolation, particularly among the islands of eastern Asia. He considered the distribution of mosses to be comparable to that of tracheophytes and assumed that bryophytes lack an effective means of long-range dispersal. He also considered that bryophytes evolve very slowly, a factor that appears to be true for their morphology but not for their biochemistry and physiology (Glime 2011), and that this lack of evolution results in most moss species having wider ranges than the tracheophytes, *i.e.*, they have not evolved into new species. This perspective made sense based on our morphological understanding of species, but forty years later, with more recent techniques, we are learning that there are DNA differences and that many disjunct or distant populations represent microspecies that differ genetically, and presumably also biochemically. Hence, bryophytes have evolved to occupy somewhat different niches as they have spread to more distant lands. It seems that these wonderful plants have conjured up a million ways to confound us!

Certainly some records confirm that bryophytes have broader distributions than do tracheophytes. Jerry Jenkins (Bryonet 6 March 2013) has observed the colonization of his own farmland and second-growth forest in New York State, USA. This area has been invaded by about 100 bryophyte species and a similar number of tracheophytes. He has found a striking contrast in the distributions of the invading species of these two groups. Approximately half of the bryophytes are species known from two or more continents, whereas most of the tracheophytes are restricted

to North America, and many to eastern North America. This leads us to examination of the concept that "everything is everywhere."

Everything Is Everywhere!

Baas-Becking (1934) formulated this hypothesis for micro-organisms, promulgating the notion that "everything is everywhere, but, the environment selects." This concept will be discussed later (Interactions volume) for protozoa and small animals. But is the concept applicable to bryophytes, where single-celled spores are among these small, airborne propagules?

The concept of everything is everywhere assumes that small propagules are able to travel the world over, but that once they arrive, they must locate in a suitable environment to survive. Santos-González (2007) discussed this concept for fungi, which, like the bryophytes, can spread by single-celled spores. It is easy enough to show for both fungi and bryophytes that the environment selects, but to demonstrate that everything is everywhere is more challenging. Not only must we demonstrate that air patterns are capable of distributing and redistributing bryophyte spores (and even asexual propagules) to all locations, but we must also demonstrate that they survive the journey. Such experimentation has rarely been attempted.

Bryophyte species are generally more widely distributed than those of tracheophytes (Pisa *et al.* 2013).

Lazarenko (1958) considered the remote transport of moss spores as doubtful in explaining the formation of discontinuous moss ranges. Rather, he, like Iwatsuki (1972), asserted that moss distribution has followed the same principles as that of tracheophytes, following continental drift theory. He uses radiation of species from two distribution centers of *Syntrichia ruralis* (Figure 24) to illustrate the role of the separation of the continents. He rejects the significance of long-distance transport to explain such patterns. While I agree that he has offered a plausible explanation, I do not agree that it is the only one, and I consider it possible that *Syntrichia ruralis* could have been transported from a northern location prior to the Ice Age to both Europe and North America or been transported at some point in time from one of those continents to the other, perhaps when the species was young, then diverged into the various lineages of similar species, resulting in several degrees of differences. Such transport could have occurred by wind passage. Nevertheless, Lazarenko argues that the ranges of mosses show the same zonal regularities as seed plants. While that may be true, many bryophytes have much wider distributions than seed plants, suggesting a different or easier mode of dispersal. Most bryologists do consider that many bryophytes are capable of long-range dispersal, accounting for the presence of many species on both sides of the Atlantic Ocean and others at both poles. Van Zanten and Pócs (1981) considered it likely that long-distance transport was common for spores under 25 μm . On the other hand, they considered transport across the equator to be difficult, if not impossible.

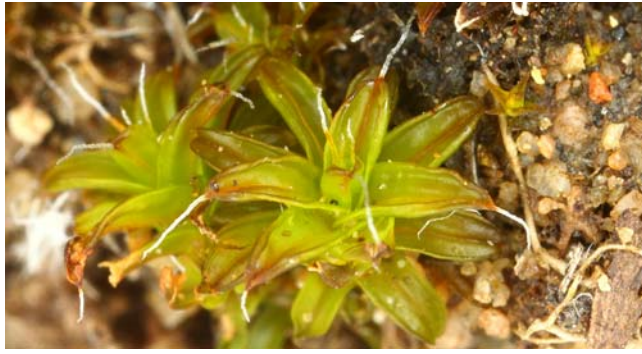


Figure 24. *Syntrichia ruralis*. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Pisa *et al.* (2013) used *Bryum argenteum* (Figure 7) to demonstrate the Baas-Becking hypothesis. This species has a wide (**cosmopolitan**) distribution. They found that genetic diversity demonstrated environmentally driven genetic variation, with the greatest genetic diversity above 1900 m. There was a significant genetic variation correlation with elevation, but the genetic diversity did not correlate with geographic distance, supporting the concept of long-distance dispersal rather than stepping-stone distribution.

Spore Size and Range

One way to test "everything is everywhere" and support or refute Lazarenko's assertion is to examine correlation between spore size and species range. This correlation remains to be done on a broad scale. And this correlation might not be instructive if nearly all bryophyte spores are small enough to travel everywhere. As Schuster (1969) concluded, the evidence of distributions seen at our present point in time does not really permit us to distinguish ancient overland dispersal from more recent dispersal by spores. Delgadillo (1993) discussed this same problem in trying to explain the bryogeographic relationships between the Neotropical flora and that of Africa, areas that share about 334 taxa. These decisions are complicated by rapid evolution vs slow evolution. It is interesting that while the Afro-American liverworts number 74 species, these are all in one family, the **Oxymitriaceae** (Figure 25) (Gradstein 2013). Nevertheless, these constitute about 5% of the Neotropical liverwort flora and 8% of the African liverwort flora. Gradstein treats these as primarily the result of long-distance dispersal.



Figure 25. *Oxymitra incrassata* (Oxymitriaceae), representing the only Afro-American liverwort family. Photo by Michael Lüth, with permission.

Distribution Stories

Schuster (1979) attempted to understand the distribution of liverworts in the Southern Hemisphere, where "old" families seem to predominate. He considered dispersal there to be the result of short-range or "step-wise" (referred to herein as "**stepping stone**") dispersal. This explanation relies on the separation of populations due to the fragmentation of Gondwanaland (Figure 26) and makes assumptions about the rate of speciation and efficiency of long-distance dispersal compared to the presumed geological background. Schuster (1982) explained the origin of plant groups in the southernmost Gondwanaland with the continental fragments (Figure 26) as "floating Noah's arks."

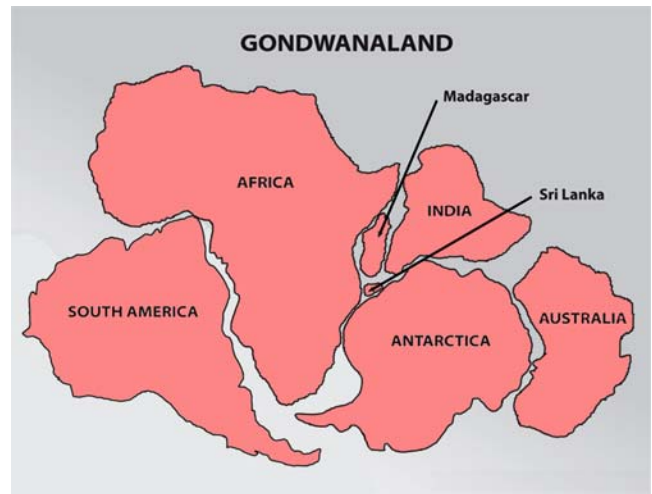


Figure 26. Gondwanaland breakup. Redrawn from Richard W. Hughes.

Ceratodon purpureus (Figure 27) arrived on one of the outer Aleutian Islands within less than a year of eruption (Rod Seppelt, Bryonet 11 March 2013). Surtsey was colonized by bryophytes by 1967 following the island's emergence from the sea off the Iceland coast in 1963 (Fridriksson & Magnússon 1992). However, the first vascular plant was found there in just two years after eruption, in 1965.



Figure 27. *Ceratodon purpureus* with capsules. Photo courtesy of GERALYN Merkey.

In New Zealand populations of *Sphagnum plumulosum* (= *S. subnitens*; Figure 28), Eric Karlin, Jon Shaw, and Dick Andrus found that only two genetic

signatures existed, representing two founding parents (Rogers 2011). In northwestern North America, they found 100% of the gene pool was derived from one individual! This means that to colonize the widespread areas in these two regions required considerable dispersal. They determined that this dispersal involved both vegetative fragments and spore dispersal. They also concluded that the spread of this species from Europe to North America and to New Zealand was by humans within the last 300 years, followed by non-human dispersal to reach their present ranges in those two regions.



Figure 28. *Sphagnum subnitens* with capsules. Photo by David Holyoak, with permission.

Island Colonization Stories

Surtsey, off the southeast coast of Iceland, provided a natural experiment in colonization following its volcanic emergence from the sea. The primary colonizers were mosses and lichens on the hardened lava and tracheophytes on ash. Colonization on Surtsey compared to Katmai in having few Cyanobacteria, but differed from Krakatau, where the primary colonizers were Cyanobacteria (Brock 1973). Tracheophytes arriving and becoming established were inversely proportional to the distance from the available source, the nearest being a rock 5.1 km away (Fridriksson 1987). However, distance to the mainland is more than 35 km.

Bryophyte invasion lagged behind that of tracheophytes. This may be the result of dispersal types, with most of the tracheophytes arriving with birds (Magnússon *et al.* 2009). Nevertheless, by 2008 on the block lava on the eastern part of the island, tracheophytes were still poorly represented. Instead, the lichen *Stereocaulon* and moss *Racomitrium* (Figure 29) predominated. By 1994, the Lesser Black-backed Gull invaded the southern barren lava and used the *Racomitrium* as nesting material. The effect of these birds in spreading the moss on the island is unknown.

The Northern Stockholm archipelago in the Baltic Sea can provide a test of dispersal and "everything is everywhere." Among the 19 islands, Sundberg *et al.* (2006) found 500 patches of *Sphagnum* in 19 species in 83 rock pools on 14 of these islands. The species richness on the islands correlated positively with island area and degree of shelter by surrounding islands, emphasizing the

importance of habitat even when other locations might be more accessible. Supporting this habitat importance, they found that distance from mainland, connectivity, height, and age did not add to the predictability of the island flora. This suggests the importance of aerial dispersal over long distances. Furthermore, spore size did not add to the model, supporting my suggestion that most bryophyte spores might be small enough to be "everywhere." However, individual species did differ in the habitats they occupied, supporting the concept of "the environment selects." Species frequency (number of colonized islands and rock pools) was predicted primarily by spore output of the species on the mainland.



Figure 29. *Racomitrium lanuginosum* on rock. Photo by Janice Glime.

The choice of *Sphagnum* from these Baltic islands is a good one to support the Baas-Becking hypothesis. *Sphagnum* has no specialized asexual reproductive structures (Sundberg *et al.* 2006), although the importance of fragmentation in this genus is poorly known. Furthermore, only 2% of the *Sphagnum* patches on the islands produced sporophytes, and these were mostly on *Sphagnum fimbriatum* (Figure 30). Hence, we can be reasonably certain that there has been little or no stepping stone dispersal (discussed below) and that colonization is the result of spore dispersal from the mainland. Sundberg *et al.* concluded that the *Sphagnum* on the island is the product of centuries of colonization, but that it is not dispersal limited.



Figure 30. *Sphagnum fimbriatum* in Europe. Photo by Michael Lüth, with permission.

Factors Contributing to Dispersal

Distance from Source

One of the most obvious factors limiting dispersal is distance to be travelled. Sundberg (2005) found that the spore deposition patterns of *Sphagnum* fit the inverse power law (deposition per unit area is proportional to the distance ($R^2 > 0.99$)). Nevertheless, when the curves were extended to infinity, they failed to account for all the spores dispersed. For example, in *Sphagnum squarrosum* (Figure 31), only 11% could be accounted for. Therefore, something else must be occurring. Sundberg suggests that this "something else" is thermal updraft.



Figure 31. *Sphagnum squarrosum* with capsules. Photo by Michael Lüth, with permission.

Sundberg (2012) used cotton cloth traps to assess the *Sphagnum* spore density in spore rain. He estimated that densities were approximately 6 million per m^2 over the season in a large area, but were only 1000 m^{-2} in Svalbard, northern Norway, indicating that all rains are not equal. Spore rain was strongly related to distance from source, especially relating to sources within 200 km. It is interesting that he found larger spores at isolated island sites, suggesting that they originated from distant, humid areas. In boreal areas, *Sphagnum* accounts for immense numbers of spores, a factor that accounts for its ability to colonize quickly in the wetlands there. Most striking to our consideration of long-distance dispersal is his estimate that 1% of the spores were of a trans- or intercontinental origin and that these spores originate from multiple locations.

Hutsemekers *et al.* (2008) used slag heap colonization to determine distances and travel rates of bryophytes. They found that 44% of the species recruited had a source within 6 km. The remaining 56% had recruitment sources within 6-86 km and arrived in less than 50 years. The weedy species were the first to arrive with the perennial stayers becoming important after 50 years.

Dispersal Pathway

Just as wind-pollinated trees are adapted to disperse their pollen in spring before the leaves come out on the trees to avoid that interference, bryophytes are limited in their dispersal by similar obstructions. Fenton and

Bergeron (2006) found that *Sphagnum* (Figure 31) spore abundance in boreal forests of northwestern Quebec, Canada, was inversely correlated with local tree stand density, and suggested that this was evidence that wind intensity may play a role in limiting dispersal. I would add to that the ability of trees to serve as spore traps.

Renner (2004, 2005) used data on direction, strength, and speed of both sea currents and wind jets to explain dispersal of plants across the tropical Atlantic Ocean. He used data from genera, partly because of data availability and partly, as he argued, because families may have broken up (evolved) before dispersal and species had too much anthropogenic influence. Nevertheless, 110 genera contain species on both sides of the tropical Atlantic. Dispersal patterns and disjunctions can be related to water currents between Africa and South America and to exceptional westerly winds from northeastern Brazil to northwest Africa. Although dispersal by water in both directions seems to be more common for these genera than wind or animal dispersal, bryologists have considered the saltwater to be lethal to bryophyte spores. Furthermore, wind dispersal seems to have facilitated spread from South America to West Africa, but not in the opposite direction.

Air Currents

Van Zanten and Gradstein (1988) summarize the air currents that can facilitate long-distance dispersal:

1. dry air streams at relatively low altitudes (<3000 m)
2. hurricanes, tropical storms, or depressions
3. wet air streams at relatively low altitude (< 3000m)
4. dry air streams at high altitudes, e.g. jet streams (ca 10,000-12,000 m asl)

These means of transport vary in their limiting factors: high UV, desiccation, wet freezing, low atmospheric pressure, ozone. The two dry airstreams subject the diaspores to desiccation, with the jet stream causing dry freezing and strong UV radiation, but the low altitude transport has only moderate UV radiation. Likewise, the wet air stream at low altitude has even lower UV radiation due to absorption and reflection by clouds. Hurricanes and storms can have wet-freezing and lower atmospheric pressure, accompanied by different air composition. These storms are likely to be less effective for long-distance dispersal because of the heavy precipitation that can clean the air of the diaspores. The wet air streams at low altitudes seem to be the safest mode of travel, with only moderate desiccation and low UV intensity.

Molecular Clocks

Molecular clocks have become useful tools to determine not only the pathway, but also the timing of transport of propagules (Renner 2005). Using molecular sequences (gene regions), one can estimate the age of a particular lineage and determine its approximate arrival time. Using fossils, models can analyze the change in substitution rates of a lineage by combining molecular data with known time constraints, particularly with fossils. These fossil/molecular "clocks" are termed **relaxed clocks**. These molecular clocks become effective tools that can be combined with information on prevailing wind and water currents, position of land mass, and size of land mass.

Weather

One might assume that wind dispersal is going to be affected by weather. Fungi might serve as a model for expectations of the effect of weather on bryophyte dispersal. In a study on fungal dispersal, Gregory and Hirst (1957) determined that airborne spore concentrations were dependent on weather and the phenology of the local flora. Lönnell (2011) considered horizontal wind speed and thermal updrafts/turbulence as factors that influence the dispersal distances.

Fungi demonstrate the importance of intermittent and gusty wind in spore dispersal (Aylor 1990). And like wind-pollinated trees, canopy plants with leaves can trap the spores and thus must be avoided unless they are indeed the target. For tropical bryophytes, this may be the case, but in temperate zones, tracheophyte leaves are rarely the target substrate. Hence, like the windborne pollen seeking a stigma, the bryophyte pollen must avoid the canopy traps in order to travel any great distance. Aylor points out the importance of gusts of wind in once again removing trapped spores and putting them back into the air. He assumes that gusts can enhance the air movement by a factor of five in the canopy compared to the average air movements. In the fungi, and likely in the bryophytes, half the spores that have ventured only a few meters from their source can escape the canopy if they are released from mid-canopy or higher. If this premise holds, then epiphytes gain considerable dispersal advantage by their high starting location.

A further simulation shows that fluid motion such as that of smoke can cause an ejection type of flow that enhances spore escape from its source. In fact, Aylor (1990) contends that movement of smoke (and similar cloud-type movements of spores) create features similar to release from the top of the canopy. Aylor suggests that the most difficult aspect to model is the "takeoff" from the source and "integration into the transport process," in the bryophyte case being from the capsule.

Fires

I must wonder if forest fires play any role in distribution. Certainly there are tremendous updrafts (Figure 32), but are there updrafts that are cool enough for diaspores to survive? Based on my observations in Yellowstone after a massive fire, I have to suspect there might be. There were patches of trees burned on one side, but live on the other, suggesting that bryophytes might also survive there but be subjected to the updrafts. But better evidence came from patches of *Pleurozium schreberi* (Figure 33) that were burned on part of a clump but green and healthy only millimeters away. Surely those nearby burned portions were creating updrafts, even if only small ones. It took only a glance at the mountainside to understand the patchiness of the burn itself. Surely these patches of fire created considerable turbulence that could thrust diaspores for considerable distances. If the soot can reach a location, so can the diaspores. And the smoke itself might offer protection from UV light. We need to examine temperature and air movement patterns to further assess the feasibility of these updrafts as dispersal agents.



Figure 32. Wildfire in California, USA. Photo through Wikimedia Commons.



Figure 33. 1989 view of *Pleurozium schreberi* next to burned soil from a 1988 fire at Dunraven Pass, Yellowstone, Wyoming, USA. Photo by Janice Glime.

Diaspore Characteristics

Not all bryophytes are created equal. Individual characteristics can determine the likelihood of the spores becoming part of the spore rain. Lönnell (2011) lists diaspore size, shape, weight, type of abscission (active or passive), abscission height, and abscission time to contribute to dispersal distances.

Most experiments on bryophyte dispersal have suffered from distance limitations of only a few meters. Lönnell *et al.* (2012) conducted a novel experiment in which they eliminated the possibility of multiple spore sources by isolating a pot of *Discelium nudum* (Figure 34) on a raised bog where its normal clay habitat was unavailable. Hence there was little possibility of other colonies contributing to the experiment. Pots of clay, numbering 2000, were placed at various distances between 5 and 600 m from the mother colony. Within 10 m of the mother colony, the mean colonization rate was greater than 50%. In the 10-50 m range, the colonization rate dropped sharply, but for pots between 50 and 600 m the colonization rate was stable, ranging 1-3%. The estimated number of spores (2-6 per m²) in that most distant segment was commensurate with the spore output of the mother colony. Lönnell considered this to be evidence that the majority of spores of this species escape the parent colony

to travel greater distances. Thus, establishment into new locations at distances measurable in kilometers is likely for this and probably a number of other species with similar spore output and dispersal characteristics.



Figure 34. *Diselium nudum* with red antheridia. Photo by David T. Holyoak, with permission.

Work by Hutsemekers *et al.* (2008) adds credence to this assertion of kilometers of dispersal. Using 52 slag heaps in Belgium as pristine soil, they tracked the invasion by bryophytes to heaps at various distances and inferred rate of dispersal by the distance and time of arrival. As expected, the number of species per slag heap is significantly correlated with area size of the heap and time since colonization. It is the weedy species that arrive first, exercising a superior dispersal ability and generally large numbers of spores.

Evidence from Geophysics

Diffusion Models

Levin (1992) contends that generalized diffusion models can explain dispersal of seeds, pollen, and even invertebrate larvae, where winds, currents, and gravity play the major roles. Even organisms that are able to use detailed environmental cues may be dispersed primarily according to diffusion models. Adding habitat-dependent movement can improve the model. Nevertheless, an adequate model can be developed on diffusion alone to explain the spread of oaks and muskrats (Skellam 1951)! However, Levin (1992) suggests that the diffusion model does not apply well on broader scales and that more refined models are needed. He lists the percolation model for fragmented habitats (Gardner *et al.* 1987; Durrett 1988), the correlated random walk for the movement of insects (Kareiva & Shigesada 1983), or clonal growth for branching organisms (Cain 1990, 1991).

It is likely that models mentioned by Levin (1992) apply as well to a number of bryophyte species. Certainly clonal growth is common among bryophytes and can account for small-scale distribution patterns. The percolation model or the correlated random walk may account for distribution of **Splachnaceae** (dung mosses; Figure 35-Figure 36), where the fly may follow a random pattern of visiting dung piles, but the moss dispersal would be closely correlated to that pattern. It would seem as if these fly-dependent taxa might disperse in a manner similar to that of host-specific parasites.



Figure 35. *Splachnum ampullaceum* capsules on dung in southern Europe. Photo by Michael Lüth, with permission.



Figure 36. Fly visiting capsules of *Tayloria mirabilis* near Cape Horn. Photo by Adam Wilson NYBG, through public domain.

Numerous phytogeographic papers have suggested dispersal patterns over broad areas and linked modern distribution patterns to earlier geologic events. Since major air movement patterns are known, and Van Zanten's work (1975, 1976, 1977a, b, 1978a, b, 1983, 1984, 1985, van Zanten & Gradstein 1987, 1988, van Zanten & Pócs 1981) provides us with data on aerial survivorship of a number of species, it should be possible to test the diffusion model on bryophytes.

Dust Storms

In their discussion of the global transport of dust, Griffin *et al.* (2002) describe the massive movement of bacteria, viruses, and fungi along with suspended dust particles (and soil pollutants). Just as an example, they estimate that about 13 million metric tons of sediment from Africa land in the North Amazon Basin of South America in a year. Just one dust storm can deliver 200 metric tons.

Charles Darwin, in 1846, expressed the situation as follows: "From the several recorded accounts it appears that the quantity of dust which falls on vessels in the open Atlantic is considerable and that the atmosphere is often rendered quite hazy; but nearer to the African coast the quantity is still more considerable. Vessels have several

times run on shore owing to the haziness of the air; and Horsburgh recommends all vessels, for this reason, to avoid the passage between the Cape Verd Archipelago and the main-land." (in Griffin *et al.* 2002). Miles Berkeley (in Griffin *et al.* 2002) concluded that the trade winds could carry fungal spores for thousands of kilometers. German scientists, in 1908, found that the most common bacteria were highly pigmented and all were spore-forming (Griffin *et al.* 2002), suggesting adaptations for aerial dispersal. By 1921, the record height for finding viable bacteria was 21 km above the earth. But these collections had been over land. Finally, in the mid 1930's, Fred Meier, a scientist with the U.S. Department of Agriculture, persuaded Charles Lindbergh to contribute to our knowledge by flying a plane with a metal arm holding microscope slides with a sterile coating of oil while he flew over uninhabited ice, water, and mountains from Maine, USA, to Denmark. These collections revealed fungal spores, pollen, algae, diatoms, and insect wings. Meier then planned sampling over the Caribbean Sea and the Pacific Ocean, but he died in a plane crash in 1938 while doing fieldwork. All these data suggest that bryophytes, too, could enter the jet stream and accomplish long-distance travel.

Not All Storms Are Equal

The next important revelation was that storms of tropical origin were far more likely to enter the upper atmosphere than those of polar origin, carrying nearly 100 times as many fungal spores (Griffin *et al.* 2002). Microbes in the dust in the Virgin Islands show a ten-fold increase during African dust storms. Then a new record for height was set – 77 km above the Earth's surface for some pigmented fungal spores. Of more relevance to the bryophytes is the presence of pollen grains, which might be expected to have similar size and structure to that of bryophyte spores, at 17-19 km above the Earth. This understanding of particle movement is important to our understanding of bryophyte distributions, helping to explain why some tropical bryophytes may appear in polar geothermal areas.

Aloina Example

Numerous authors have attested to the long distance travelling capabilities of bryophyte spores. Kimmerer (1991) found that many spores were trapped 2 m from the plants and contended that spores ensured long-distance dispersal. Pettersson (1940) filtered spores from precipitation in Finland, then grew them to identify them. Large numbers of spores from *Aloina brevirostris* (Figure 37) were present, as well as those of *A. rigida* (Figure 38), but the genus *Aloina* was unknown in Finland. Both species prefer calcareous substrata and thus are limited in their distribution. Pettersson suggested that they came from Siberia, citing the absence of *A. rigida* in nearby European countries, but Persson (1944) and Bergeron (1944) both rejected that hypothesis.

Persson argued that Pettersson ignored the other species that accompanied the *Aloina* (Figure 38). Among these, *Bryum pallens* (Figure 39), *Leptobryum pyriforme* (Figure 40), and *Marchantia polymorpha* (Figure 41) present no problem, all being common in both Europe and Siberia. However, *Metzgeria* was not known from Siberia,

although *Echinomitrium furcatum* (= *Metzgeria furcata*) (Figure 42) is common in Europe. Persson's second argument was that the *Aloina* spores were quite common in the rain (est. at least 60,000,000,000 / km²). That would be an incredible number to come from such a distance as Siberia. The final complication was that an *Aloina* from neighboring European countries had been misidentified as *Aloina ambigua* when in fact it was *Aloina rigida* (Figure 38), making a European origin of *Aloina rigida* quite possible; furthermore, he considered identification of *Aloina rigida* without capsules to be difficult, if not impossible.

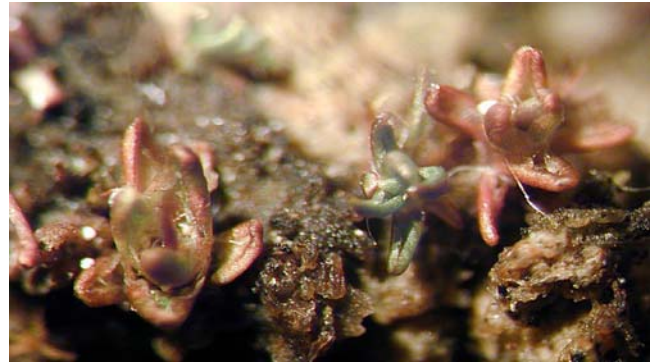


Figure 37. *Aloina brevirostris* gametophytes. Photo by Michael Lüth, with permission.



Figure 38. *Aloina rigida* gametophytes and sporophytes. Photo by Michael Lüth, with permission.



Figure 39. *Bryum pallens* showing red pigmented phase. Photo by David T. Holyoak, with permission.



Figure 40. *Leptobryum pyriforme* with capsules. Photo by Michael Lüth, with permission.



Figure 41. *Marchantia polymorpha* with gemma cups. Photo by Michael Lüth, with permission.



Figure 42. *Echinomitrium furcatum* (= *Metzgeria furcata*) in Europe. Photo by Michael Lüth, with permission.

Bergeron's (1944) arguments against a Siberian origin for the *Aloina* (Figure 38) were meteorological rather than biological. First, the weather conditions in Siberia during the preceding week were not likely to have had the force needed to bring the spores into the airstream where they were needed to travel to Finland. Second, rather, the air masses arriving on the day in question originated to the north from other European countries. Third, the air masses leaving the Siberian region did not travel in the direction of Finland. Fourth, the conditions at the collecting site in Finland on the days of sampling did have the right weather

conditions to bring down spores, and these were most likely to have come on air currents from the NNW or SSE, either of which would have traversed areas where *Aloina* grows and neither of which would have passed over Siberia or joined forces with air from that region. There are lots of factors to consider when attempting to determine the origin of propagules.

Size and Falling Velocity – Distance and Laws of Physics

The first condition of passive dispersal by wind for a diaspore is to get caught by the wind before reaching the ground. For the tiny distances that bryophyte diaspores fall to their substrate, this is a challenge. The laws of physics would predict that atmospheric density of dispersed spores will decrease with increasing distance and increasing height from the colony.

This can be helped somewhat by animals (I'm guessing especially squirrels and other rodents) that bump them and cause clouds of spores to become airborne. In rangeland, hooved mammals surely contribute. Once airborne, the falling velocity is important. Small spores like those of bryophytes typically have a falling velocity less than those of larger objects, permitting them to stay airborne longer and have greater opportunity for capture by moving air.

One approach to examining long-distance dispersal is to develop a trajectory model. Trackenberg (2003) developed such a model (PAPPUS) to consider the potential of wind as a dispersal vector. The model included effects of topography, turbulence (including thermal updrafts), and weather conditions. Simulations included initial release height and falling velocity. It improved on most approaches by modelling turbulence. The model was tested against distances measured in the field. Trackenberg considered that sunny weather with thermal turbulence and updrafts would cause a high proportion of long-distance dispersal, even in periods of low horizontal wind speed.

Not only does the model suggest that sunny weather with thermal turbulence and updrafts may be most important, Trackenberg (2003) concluded that stormy weather may have little importance for long-distance dispersal, especially for species with falling velocities less than 1.5 m s^{-1} . Horizontal wind speed seemed to have no effect on diaspores dispersing more than 100 m; frequency of updrafts was positively correlated. I became aware of this importance myself during a blizzard. I'm not suggesting that spores get distributed in blizzards, but the wind patterns can be seen then without equipment. My "aha" moment came as I watched wind and snow swirl around my house and carve a funnel in the snow, raising the snow into the airstream. While this 1 m wide funnel was caused by an L corner of my house, smaller funnels can occur around rocks and other obstructions where bryophytes grow. Snow is a good marker for wind patterns, and it is common for us to see the snow "falling" upward as wind whirls around buildings and other obstructions. Such wind conditions are not restricted to winter. If it is not a rainy day, such conditions would seem ideal for getting the spores away from the ground and putting them into the airways.

Trackenberg (2003) considered the improved predictability of his model to result not only from the addition of turbulence to the model but also to the effect of

topography. Those bryophytes that are elevated either by living on trees, rocks, or walls or by living at high elevations have a greater chance of entering the atmosphere. This improvement is in part due to the slow falling velocity of the tiny diaspores of bryophytes. With falling velocities of less than 1.5 m s^{-1} , unstable atmospheric conditions and thermal updrafts under low humidity provide the greatest contributions to dispersal. If diaspore abscission is coupled with these conditions (**xerochasy**), bryophytes can optimize their dispersal capabilities.

In their predictions for immigration into a milled peatland, Campbell *et al.* (2003) assumed that diaspores released from higher altitudes are typically exposed to greater wind velocities (Greene & Johnson 1996) and thus are likely to be carried farther. As discussed above, this probably only matters once they have been lofted into the wind stream by updrafts or other short-distance mechanisms. To determine terminal velocity, Campbell *et al.* (2003) assumed a density of 1 (Gregory 1973) and applied Stoke's law for a sphere with a low Reynolds number. They also assumed that propagules with a slower falling velocity (including bryophytes) and/or with a higher release height from the ground would have a greater probability of dispersing into the mined peatland (Campbell *et al.* 2003; Trackenberg *et al.* 2003). Trackenberg and coworkers warned against using morphology as an indicator of dispersal ability, emphasizing the importance of location of growth and consequent falling distance and upwinds as being of greater importance. For plants in general, Campbell and coworkers found that dispersal distance was most sensitive to falling velocity and weather conditions. Since bryophytes in general have slow falling velocities, we might expect weather to be of greatest importance for them.

Evidence from Restoring Peatlands

Campbell *et al.* (2003) assessed the immigration potential of plants into a mined peatland in southeastern Quebec, Canada. They selected 32 species, including both bryophytes and tracheophytes, as potential colonizers, based on presumed dispersal capabilities. They developed an index of immigration potential based on:

- propagule release height
- falling time (propagule release height/settling velocity)
- propagule wing loading (probably not applicable to bryophyte spores, but possibly to gemmae and bulbils).

Their evidence supported these attributes. Those bryophytes with the higher immigration potentials by wind were usually the more frequent colonizers in the mined peatlands. *Sphagnum capillifolium* (Figure 43) and *Sphagnum fuscum* (Figure 44), however, were exceptions, with less than a 1% occurrence but relatively high immigration potential. Campbell *et al.* (2003) attributed this to an establishment problem. Rochefort (2000) found that *Sphagnum* is particularly vulnerable to drought and the instability of the substrate in the early establishment stages. But Campbell *et al.* found that mosses in general had less of a recolonization constraint than did the herbaceous species in this environment.



Figure 43. *Sphagnum capillifolium*. Photo by Michael Lüth, with permission.



Figure 44. *Sphagnum fuscum*. Photo by Michael Lüth, with permission.

Disjunct Distributions

The large number of disjunct taxa in the Andes and Atlantic coastal region of Brazil might lend support to the air current hypothesis (Gradstein & Reiner-Drehwald 2007). Major flyways for birds, especially raptors, often follow mountain ridges because these areas often have air currents that propel the birds forward, saving energy on long migrations. It is reasonable to assume they can similarly provide "flyways" for bryophyte diaspores.

Directional (**anisotropic**) dispersal seems to play a role in Southern Hemisphere distribution. Using data from global winds coverage from the National Aeronautics and Space Administration SeaWinds scatterometer, Muñoz *et al.* (2004) found that the correlation of floristics of bryophytes, lichens, and ferns with wind patterns and wind connectivity is stronger than the correlation with geographic proximity, suggesting that spores travel with the wind.

There seems to be an interesting contrast between the arrival of two species of bryophytes [*Ulota phyllantha* (Figure 45) and *Sanionia uncinata* (Figure 46)] on Macquarie Island in the Antarctic. *Sanionia uncinata* has spores only 10-18 μm in diameter, whereas *Ulota phyllantha* has cigar-shaped spores 100 μm long. As Rod Seppelt pointed out on Bryonet (6 March 2013), *U. phyllantha* occurs abundantly on the coastal rocks along the western side of Macquarie Island (Antarctica) but is rarely seen on the east coast. Its distribution on the island has led to the assumption that it has been distributed by the jet stream from southern South America. On the other hand, *Sanionia uncinata* appears to have migrated to Macquarie Island from Australia or New Zealand,

matching their genotypes, and differing genetically from other subAntarctic island populations to the east that seem to match the southern South America-Antarctic Peninsula genotypes (Lars Hedenäs, Bryonet 6 March 2013). This migration, contrary to prevailing winds and having a larger dispersal unit, suggests that dispersal by wind will not always follow prevailing winds. Wind directions do change, and Rod Seppelt (Bryonet 6 March 2013) explained that cyclonic low pressure cells can center off the southwest side of Tasmania, pass through the southeast mainland Australia, miss New Zealand and reach to the Ross Sea area of Antarctica. These heavy winds are likely to carry all sorts of propagules from Australia and New Zealand to Antarctica, thousands of kilometers away. Furthermore, during drought periods, huge dust clouds in Australia can reach New Zealand, no doubt carrying spores along with the dust.



Figure 45. *Ulota phyllantha* with capsules. Photo by David T. Holyoak, with permission.



Figure 46. *Sanionia uncinata* with capsules. Photo by David T. Holyoak, with permission.

Shaw (1982) provides us with more convincing evidence of "everything is everywhere" and the flyway hypothesis. The rare circumboreal *Plagiobryum zieri* (Figure 47) has been found in the Huehuetenango Province of Guatemala, far from its nearest neighbor in Colorado, USA. Shaw suggested that the tendency of the spores in this species to remain in tetrads may be a preadaptation to

its ability to survive such long-distance travel and become established in its high altitude homes.



Figure 47. *Plagiobryum zieri* from southern Europe. Photo by Michael Lüth, with permission.

Such disjunctions as 28 species of bryophytes common to Central America and the Himalaya Mountains (Sharp 1974) likewise lend credence to long distance dispersal of bryophyte diaspores. They not only support "everything is everywhere," but also emphasize the importance of the "environment selects."

Finding a species at both poles of the Earth tends to make one think of long-distance dispersal, and *Pohlia nutans* (Figure 48) not only supports the concept that "everything is everywhere," but it clearly supports the "environment selects." Present in Iceland in geothermal areas, common in the Northern Hemisphere, and present on the geothermal areas of the continent of Antarctica, it is the epitome of the environment selects because it is absent in other (non-geothermal) habitats in Antarctica (Skotnicki *et al.* 2002). The Antarctic populations of *P. nutans* exhibit low levels of genetic diversity (RAPD & DNA sequences of conserved nuclear ribosomal RNA), supporting the conclusion that they have been derived from a single dispersal event leading to vegetative growth, mutation, and stepping stone dispersal within the continent, a pattern also discernible for the geothermal *Campylopus pyriformis* (Figure 21, Figure 49).



Figure 48. *Pohlia nutans* with abundant capsules. Photo by Michael Lüth, with permission.



Figure 49. *Campylopus pyriformis* with capsules. Photo by Michael Lüth, with permission.

Lewis Smith (1991) considered southern South America to be a continuous source of diaspores for the Antarctic and attributes this to relatively frequent storms that track eastward over the southeast Pacific Ocean. They gain momentum over the southern part of South America where they pick up spores. Sometimes a blocking anticyclone over the South Atlantic Ocean deflects the winds, sending them off to Antarctica.

Perhaps the best explanation is one from Schofield and Crum (1972), that continental drift, long-distance dispersal, and fragmentation of a previously continuous landscape all have been considered meritorious explanations. But "no single hypothesis is sufficient to accommodate all species within any disjunctive pattern." Nevertheless, many of the bryophyte disjunctions are similar to those of tracheophytes, suggesting that similar mechanisms are at play.

Long-range dispersal in bryophytes is supported primarily by their distribution patterns and our knowledge of air movement patterns and the ability of updrafts to carry particles of various sizes. Survival of a number of taxa at atmospheric low temperatures and UV radiation suggests that such long distances may occur, but probably infrequently.

Stepping Stones

It is likely that many species disperse through relatively short distances most of the time, reaching distant locations eventually through a series of dispersal events from location A to location B, then from location B to location C, a means I shall call **stepping stones**, as that term has been used in the literature several times.

At least in some species, we can document evidence of a stepping stone means of species range expansion. For example, Derda and Wyatt (1999b) found that *Polytrichum commune* (Figure 50-Figure 51) had a high mean genetic identity between populations (0.867-0.998), but that there was significant differentiation among regions that increased with distance. This, coupled with region-specific genotypes, suggested that this species dispersed from location A to location B and then from location B to location C, *i.e.*, the "stepping stone" method. At the same

time, some distant populations had multilocus genotypes that were very similar, suggesting that an occasional long-distance dispersal event had occurred.



Figure 50. *Polytrichum commune* in its typical abundance, facilitated by new shoots from rhizomes. Photo by Christopher Tracey, through Creative Commons.



Figure 51. *Polytrichum commune* with abundant capsules that provide spores for long-distance travel. Photo by David T. Holyoak, with permission.

Bischler and Boisselier-Dubayle (1997) provide us with an example that supports the concept of stepping stones. They found that in liverworts, there are few differences among the alleles within a population. Rather, intrapopulation differences are more typically an expression of phenotypic plasticity. But over a larger area, a species typically consists of a series of small populations that are reproductively isolated from each other, presumably due to dispersal limitations on the sperm. They considered that these facts are consistent with repeated dispersal and founder events. Further variation can arise from genetic drift. They found a contradiction in the restricted gene flow between populations and the limited genetic differences among geographically disjunct populations.

Could it be that rather than stepping stones or multiple dispersal events there could have been a single event that left a number of isolated founder populations that were further divided by genetic drift? Such a proposal is not unreasonable. We know that certain weather events can carry dust for long distances [for example from the Sahara

in Africa to Texas in the USA or to California, USA (Reardon 2013) or to southern England (Ken Adams, Bryonet 6 March 2013)] or change the usual direction of weather patterns. Tornadoes can certainly pick up propagules and drop them off in a number of distant locations, sometimes far distant. Hurricanes can make similar deposits, particularly on oceanic islands. Bischler and Boisselier-Dubayle (1997) point out that liverworts have lower levels of genetic variability than do mosses. Rather, they seem to respond to habitat variation by more non-genetic responses through plasticity. Although they consider this to support a history of repeated dispersal and founder events, it does not rule out the possibility of a single dispersal event populating a number of isolated locations, then differing due to genetic drift, founder principle, or subsequent genetic modification. Their success may be due to a genetic complement that permits phenotypic plasticity.

Disjunct distributions always raise questions as to their causes – extinctions, land drift, or incomplete dispersal? Delgadillo (1987) reported that there is evidence of "extensive floristic exchange" in Mexico among the major alpine areas of the Neovolcanic Belt. However, floristic differences and ages among the mountains indicate that dispersal has not been unidirectional nor occurring through a single event. This would seem to indicate that it is not a **flyway** unless air currents change directions, perhaps with seasons. Nevertheless, this range of mountains seems to have provided a **barrier** to the dispersal of some mosses in a north-south direction, but not in the opposite direction. This might be interpreted as an example of "the environment selects," but more ecological information is needed to support that conclusion. In any case, it is likely that mountains present barriers to species that disperse through "stepping stone" pathways and that are unable to survive the climate of the mountain tops.

Dispersal by birds for any instance seems to be discounted by many researchers for a number of regions. Cruden (1966) sums up some of the concerns for transport of seeds:

1. Internal carriage is highly unlikely because it takes at least a month for migration from, for example, California, USA, to Chile, whereas the gut contents are dispelled within a few hours.
2. External carriage is likewise unlikely because the birds frequently preen themselves.
3. The disjunct plant groups do not seem to have any special qualifications for long-distance dispersal. Rather, they live in open, unstable habitats; their seeds can be dispersed by animals; and they are self-compatible.

But some of the objections applied to bird dispersal for tracheophytes do not seem to apply as well to bryophytes. It is unlikely that internal carriage of bryophyte diaspores occurs on long flights, but it could occur in a stepping stone fashion. External carriage is more likely. If a bird in fact walked through a patch of dispersing capsules, numerous spores could adhere. Because of their fine nature and small size, it seems unlikely that preening could remove all of them, and some are also likely able to continue adherence even through the splashing of a bird's bath. Furthermore, like seed plants, only a single spore is needed in the right

place to begin a new population, and the birds are likely to seek out the same kind of habitat as the one where the spore first joined the journey, *i.e.*, a suitable habitat. Cruden (1966) has noticed a correspondence between wintering areas of the birds and plant distributional ranges. He likewise suggests that mountain hopping has been undervalued as a possible migrational route for the plants, in some cases at least following the flyways of the birds. Whereas shorebirds seem to satisfy the long-distance requirements, mountain hopping could account for distribution by a larger number of birds. This latter mechanism could follow the long-distance travel on a shore bird, and at least for bryophytes, seems like a plausible mechanism.

Gene Flow

Gene flow is an indirect measurement of dispersal. While it cannot tell us distance values, it can suggest the magnitude of gene dispersal, hence spore dispersal (assuming that spore dispersal is greater than gamete dispersal). Gene flow results in increased genetic variation within the population and prevents that population from exhibiting genetic differentiation from other populations. For *Leucodon temperatus* and *L. luteus*, both epiphytes, the gene diversity between populations relative to the total diversity was low (Akiyama 1994). Akiyama interpreted this as evidence of extensive gene flow between populations. He considered the low genetic divergence to be a result of their epiphytic habitat, which would suggest that lots of new invasions by spores occurred.

Genetic diversity can be maintained even as a result of small remnant populations in *Trichocolea tomentella* (Figure 52). The apparent infrequent gene flow among populations of this species indicates that it suffers dispersal limitations, even on a small spatial scale. On the other hand, new colonization within a population is not affected by its isolation, suggesting that it benefits from random short-range dispersal of fragments. It furthermore appears to have a long life span that permits it to spread through branching. On the other hand these characteristics suggest that it is not a good colonizer because of its limited dispersal.



Figure 52. *Trichocolea tomentella*, a leafy liverwort. Photo by Michael Lüth, with permission.

Korpelainen *et al.* (2005) evaluated gene flow in bryophytes in a broader context. They found that most bryophyte species (*i.e.*, mostly mosses) have a fair amount of gene flow between populations, based on the genetic differentiation that exists among populations. That suggests that there is a fair amount of invasion of populations by spores of other populations.

On the other hand, Derda and Wyatt (1990, 1999a, b) found genetic evidence in *Polytrichum* species to indicate that distribution of genetic variation by spores was limited. For *P. commune* (Figure 50-Figure 51) the mean genotypic diversity was 0.546. For *P. piliferum* (Figure 53) the mean genetic diversity within populations was only 0.037 (Derda & Wyatt 1999a), whereas in *P. commune* it was 0.061 (Derda & Wyatt 1999b). Derda and Wyatt (1999b) concluded that long distance dispersal did occasionally occur, based on "region-specific multilocus genotypes" that occasionally occurred distant from the apparent parent population. The fact that this species has a worldwide distribution suggests it is capable of at least some long-distance dispersal. More commonly, it appeared that genotypes moved from location to location in a "stepping-stone" fashion. As one would expect, the genetic similarities between regions generally decreased with the distance between the regions. Evidence from *Polytrichum juniperinum* (Figure 54) and *P. strictum* (Figure 55) suggests that dispersal distances and gene flow may depend in part on latitude (Derda & Wyatt 2003). For *P. juniperinum*, Derda and Wyatt found that spore dispersal in the upper Midwest and Pacific Northwest of the USA and Canada was apparently low and relatively less effective south of the Pleistocene glacial margins, whereas colonization from distant refugia seems to have been more effective in the northern latitudes. Members of the *Polytrichaceae* are unique in having an **epiphragm** stretched across the peristome teeth, providing only tiny holes from which spores can be dispersed (Figure 56). Van Zanten (1973) considered that long-range dispersal was unlikely in the *Polytrichaceae* genus *Dawsonia* (Figure 10), citing horizontal spore ejection by raindrops or other agents that strike the mature capsule. It is likely that other members of the family suffer the same problem.



Figure 53. *Polytrichum piliferum* with young capsules. Photo through GNU free documentation license.

Polytrichum strictum (Figure 55), a species that has often been treated as a subspecies of *P. juniperinum* (Figure 54), has some of the highest gene diversity levels

known for mosses (HTP = 0.205), with strong regional partitioning of the genetic structure (Derda & Wyatt 2003). This might be explained by the lack of re-invasion of spores into a colony, permitting genetic drift and gene divergence. This lack of re-invasion is consistent with the poor spore dispersal predicted by Van Zanten (1973).



Figure 54. *Polytrichum juniperinum*. Photo by Li Zhang, with permission.

The story for *Hylocomium splendens* (Figure 57) in Scandinavia seems to be quite different from that of *Polytrichum* (Figure 53-Figure 56). Cronberg *et al.* (1997) found that among populations from four vegetations zones, eleven out of thirteen loci screened by allozyme electrophoresis demonstrated variation. The relative differentiation among the populations was low ($G(ST) = 0.073$), indicating a high level of gene flow between populations. Furthermore, although the Subarctic-alpine population was apparently a single widespread clone, it was comprised of many rare genotypes that often occurred together within 10 x 10 cm patches. Cronberg *et al.* concluded that this population had spread by dispersal of vegetative fragments. In the lowland populations, identical genotypes often occurred in multiple patches, which Cronberg *et al.* interpreted to indicate that these had arisen by independent sexual recombinations, not dispersal. Hmm...Why not by fragments?



Figure 55. *Polytrichum strictum* with male splash cups. Photo by Kristian Peters, through GNU free documentation license.

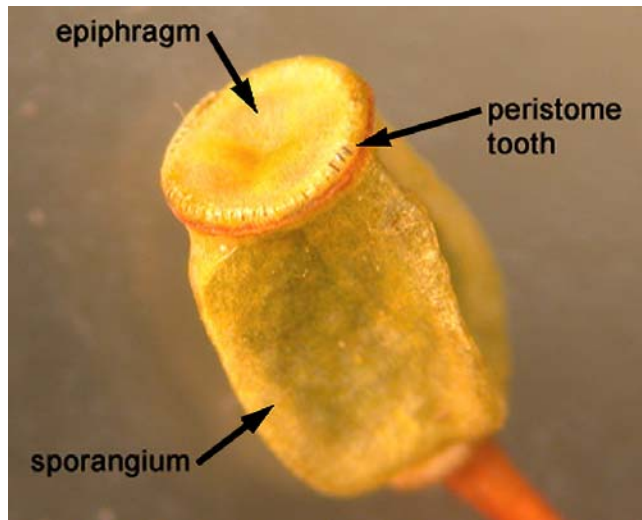


Figure 56. Capsule of *Polytrichum commune* showing epiphragm stretched across the 64 short teeth. Photo with permission from Botany Website, UBC.



Figure 58. *Pleurochaete squarrosa* wet. Photo by David Holyoak, with permission.



Figure 57. *Hylocomium splendens*. Photo by Daniel Mosquin, with permission.

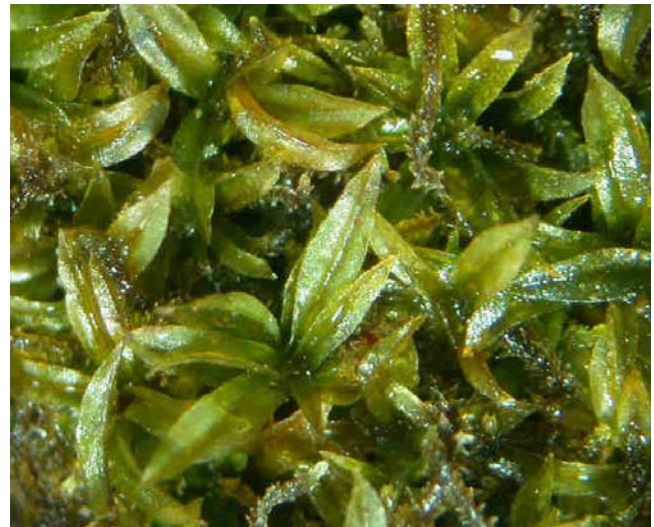


Figure 59. *Scopelophila cataractae*, a species that seems to have spread by long-distance dispersal. Photo by David T. Holyoak, with permission.

It appears that even annual shuttle species that would seemingly rely on dispersal of much more than a few meters may have little genetic mixing between populations. Roads and Longton (2003) found no field germination of spores in *Tortula acaulon* (= *Phascum cuspidatum*; Figure 4) and spores only inconsistently produced gametophytes in *Tortula truncata* (as *Pottia truncata*; Figure 2). As discussed above for the latter species, 67% of the spores never left the clump and 70% were deposited within 2 m. Nevertheless, that left 30% to be deposited farther away. However, there were no genotypes in common between populations and no variation within populations, suggesting that all members of the population had come from a single spore or clone.

Grundmann *et al.* (2007) obtained what seems like conflicting data for *Pleurochaete squarrosa* (Figure 58). Using allozymes, they showed no isolation by distance, but using DNA sequence data instead, there was evidence of isolation based on distance. Shaw (1995) used 15 allozyme loci to assess *Scopelophila cataractae* (Figure 59) and concluded that it was native to both America and Asia, having spread by long-distance dispersal.

Many bryophytes exhibit little variation within populations and reasonable variation between populations, suggesting that most within-population members are derived from the same clone. Genetic differences between populations suggest that most have arisen by a single invasion of a single propagule.

Spore Size and Number

Size matters. Aerosols – particles suspended in air like those in smoke – disperse easily to great distances, but the particles typically have a diameter less than 5 μm (Lönnell 2011). Size affects the terminal velocity of falling objects, with increasing size causing a greater terminal velocity (Lönnell 2011). But does this have any meaning for a bryophyte propagule? And if so, how is it affected by updrafts, vortices around the substrate, hydration, or surface ornamentation?

There seems to be an assumption that dispersal declines rapidly as diaspore size increases. As Frahm (2009) reminds us, bryophyte spores, typically only one cell, mostly range in size from 7 μm to 100 μm . Schmidt (1918) considered that spores smaller than 20 μm are easily dispersed, a position supported by van Zanten and Pócs (1981) who thought the small spore size permitted them to lift into the air column more easily. Mogensen (1981) tells us that theoretically, wind that would carry a 20 μm spore for 1000 km would only carry a 55 μm spore approximately 40 km. But experimental evidence for this seems to be lacking, and the large spore size of some ephemeral taxa, such as *Ephemerum* (Figure 60-Figure 61), would seem to suggest that occasionally these large spores do travel. In fact, van Zanten and Gradstein (1988) found no correlation between spore size and species range for neotropical liverworts. They cited three species with some of the largest spores [*Brachiolejeunea phyllorhiza*, *Cheilolejeunea uncioloba*, and *Leucolejeunea xanthocarpa* (Figure 62) as having transoceanic distribution

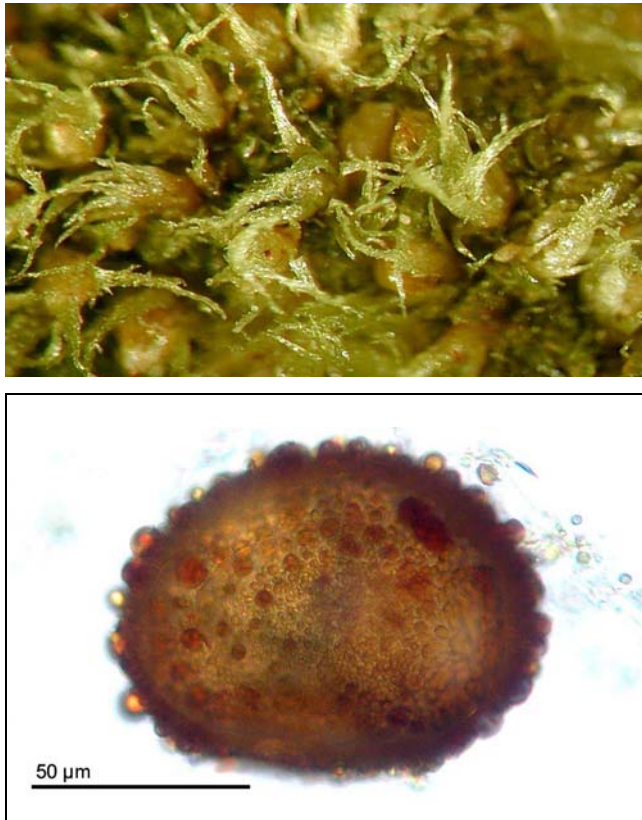


Figure 60. *Ephemerum serratum*. **Upper:** Leafy gametophytes with capsules. **Lower:** One spore. Photos by Michael Lüth, with permission.

In describing dispersal of testate amoebae in the Arctic and Antarctic, Wilkinson (2001) found that the large species (up to 230 μm) were confined to only one of those areas, whereas the cosmopolitan species had a maximum size of 135 μm . Size matters. The same principle of smaller travels farther should be applicable to bryophyte propagules. But most bryophyte spores have a diameter that is less than 50 μm (Lönnell 2011; Figure 63), with liverworts generally having larger spores than mosses, presenting a greater number of species with spore diameters in the 40-100 μm range than do mosses. Among

the species for which I could easily find numbers, the liverworts tended to produce fewer spores than the mosses, a factor one might expect to accompany larger spores (Table 2).

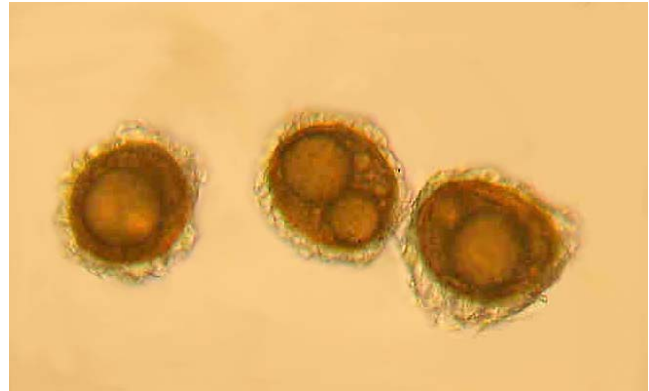


Figure 61. *Ephemerum serratum* (formerly *E. minutissimum*) spores. Photo by David T. Holyoak, with permission.



Figure 62. *Leucolejeunea xanthocarpa*, a transoceanic species with large spores. Photo by Jia-Dong Yang, through Creative Commons.

Despite the widespread assumption that small spores lift more easily, hence disperse more easily, than large spores (Van Zanten & Pócs 1981), there seems to be no empirical evidence for the assumption (McIntosh (1997). McIntosh points out that producing smaller spores permits production of more spores, and just by that increase, the probability of going farther increases.

In their examination of 24 Asian bryophytes, He and Zhu (2010) concluded that mosses have a higher spore output than liverworts (Table 2). They further observed an inverse relationship between spore size and spore number, a conclusion also supported by Lönnell (2011; Figure 64). This is especially borne out in the genus *Archidium* (Figure 22), which may have as few as four spores and these are the largest found among bryophytes (Crum 2001).

Noguchi and Miyata (1957) asserted that mosses that have abundant spores can have wide geographic ranges, but tend to have rather confined habitats. This relationship might relate to spore size, with small spores being more abundant than larger ones. And small spores do not bring with them the nutritional reserve that could give them a good start in their new location. Could this be the explanation for their "confined habitats?"

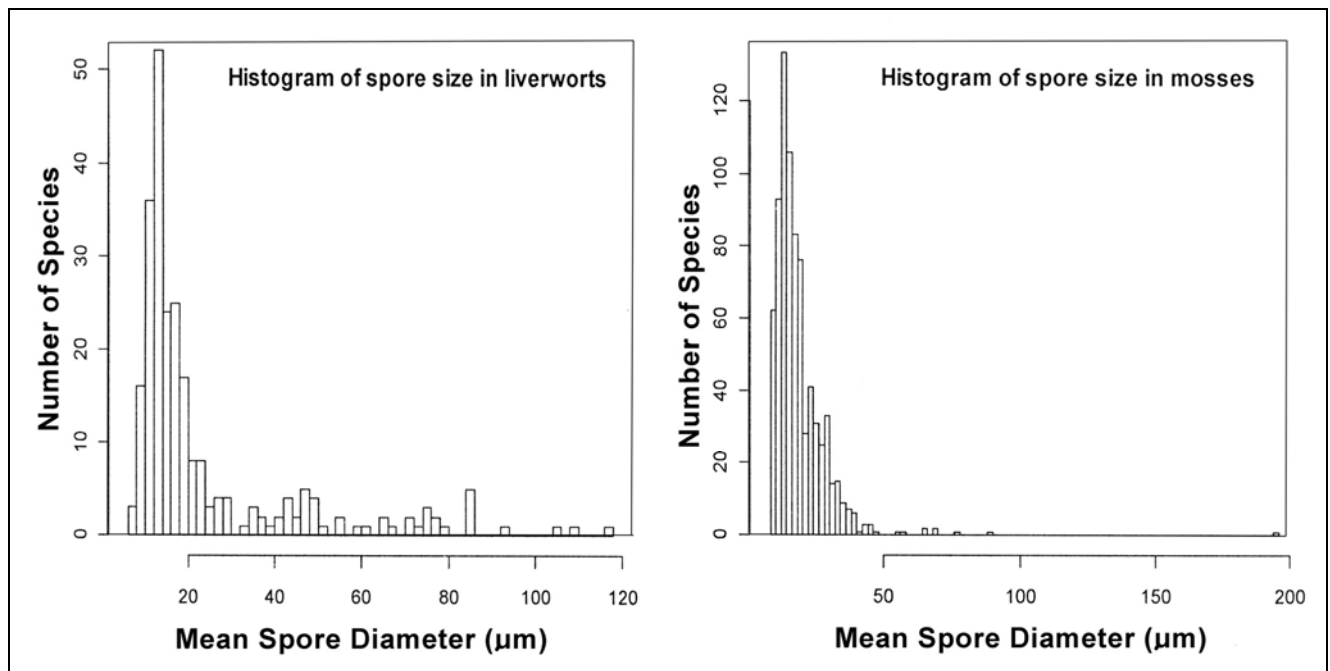


Figure 63. Comparison of spore size distributions in liverworts and mosses. Redrawn from Lönnell 2011.

Table 2. Numbers of spores per capsule in a variety of bryophytes. Liverwort taxa are in bold face.

<i>Archidium</i>	4-28	Ingold 1959	<i>Dicranella varia</i>	71,450	He & Zhu 2010
<i>Riccia gougetiana</i>	192	Schuster 1966	<i>Ditrichum pallidum</i>	79,160	He & Zhu 2010
<i>Riccia glauca</i>	220	Schuster 1966	<i>Jungermannia truncata</i>	84,150	He & Zhu 2010
<i>Riccia crystallina</i>	246	Schuster 1966	<i>Trematodon longicollis</i>	85,800	He & Zhu 2010
<i>Leptocolea</i> (=Cololejeunea)			<i>Lophozia ventricosa</i>		
<i>magnilobula</i>	257	He & Zhu 2011	var. <i>silvicola</i>	86,000	Laaka-Lindberg 2000
<i>Sphaerocarpos michelii</i>	760	Schuster 1966	<i>Chiloscyphus profundus</i>		Jonsson & Söderström 1988
<i>Acrolejeunea emergens</i>	<1000	He & Zhu 2011	= <i>Lophocolea heterophylla</i>	93,000	
<i>Trocholejeunea sandvicensis</i>	1450	He & Zhu 2010	<i>Orthocaulis</i> (=Barbilophozia)		Jonsson & Söderström 1988
<i>Fossombronina foveolata</i>			<i>attenuata</i>	115,000	
var. <i>cristula</i>	1660	He & Zhu 2010	<i>Sphagnum lindbergii</i>	129,545	Sundberg 2002
<i>Sauteria alpina</i>	2100	Schuster 1966	<i>Sphagnum palustre</i>	130,000	He & Zhu 2010
<i>Reboulia hemisphaerica</i>	2500	Schuster 1966	<i>Ceratodon purpureus</i>	100,000-120,000	Kreulen 1972
<i>Monosolenium tenerum</i>	3160	He & Zhu 2010	<i>Grimmia pulvinata</i>	200,000	Ingold 1959
<i>Pellia epiphylla</i>	4500	Schuster 1966	<i>Sphagnum squarrosum</i>	243,000	Sundberg & Rydin 1998
<i>Ptychanthus striatus</i>	5038	He & Zhu 2011	<i>Tetraplodon angustatus</i>	250,830	He & Zhu 2010
<i>Conocephalum conicum</i>	5300	Schuster 1966	<i>Rhynchostegium serrulatum</i>	280,000-700,000	Ingold 1959
<i>Tortula acaulon</i>			var. <i>confertum</i>	250,000-750,000	Ingold 1974
<i>Phascum cuspidatum</i>	5500	Ingold 1959	<i>Tetraphis pellucida</i>	348,300	He & Zhu 2010
<i>Preissia quadrata</i>	8000	Schuster 1966	<i>Scapania</i> (=Diplophyllum)		
<i>Targionia hypophylla</i>	1196-7385	Patidar <i>et al.</i> 1987; He & Zhu 2010	<i>albicans</i>	400,000	Schuster 1966
<i>Physcomitrium courtoisii</i>	8760	He & Zhu 2010	<i>Polytrichastrum alpinum</i>	440,000-873,000	Convey 1994
<i>Anthoceros agrestis</i>	>17,000	Bisang 2001	<i>Atrichum undulatum</i>	450,000	Ingold 1959
<i>Sphagnum tenellum</i>	18,500	Sundberg & Rydin 1998	<i>Funaria hygrometrica</i>	55,800-495,000	Nakosteen & Hughes 1978; He & Zhu 2010
<i>Pohlia elongata</i>	20,700	He & Zhu 2010	<i>Polytrichastrum sexangulare</i> var. <i>vulcanicum</i>		
<i>Cephalozia varians</i>	14,000-23,750	Lewis Smith & Convey 2002	(= <i>Pogonatum sphaerothecium</i>)	516,200	He & Zhu 2010
<i>Lophocolea cuspidata</i>	23,900	Schuster 1966	<i>Dicranum scoparium</i>	523,500	He & Zhu 2010
<i>Reboulia hemisphaerica</i>	25,000	Schuster 1966	<i>Haplcladium microphyllum</i>	675,830	He & Zhu 2010
<i>Ptilidium pulcherrimum</i>	27,400	Jonsson & Söderström 1988	<i>Pogonatum dentatum</i>	712,000	Ingold 1959
<i>Schistostega pennata</i>	36,000	Ingold 1959	<i>Scapania undulata</i>	1,000,000	Schuster 1966
<i>Anastrophyllum hellerianum</i>	42,000	Pohjamo & Laaka-Lindberg 2003	<i>Tortula muralis</i>	1,000,000	Ingold 1959
<i>Sphagnum rubellum</i>	54,000	Sundberg 2002	<i>Polytrichum juniperinum</i>	1,400,000	Kreulen 1972
<i>Riccardia</i> sp.	56,400	He & Zhu 2010	<i>Buxbaumia viridis</i>	1,000,000-9,000,000	Wiklund 2002
<i>Sphagnum papillosum</i>	62,250	He & Zhu 2010	<i>Polytrichastrum formosum</i>	2,200,000	Ingold 1959
<i>Sphagnum junghuhnianum</i>	68,750-73,300	He & Zhu 2010	<i>Buxbaumia aphylla</i>	5,500,000	Ingold 1959
			<i>Polytrichum commune</i>	8,983,000	He & Zhu 2010
			<i>Dawsonia lativaginata</i>	80,000,000	Kreulen 1972

Lönnell (2011) compared spore sizes among spore-producing organisms, considering those of bryophytes to range 10-50(-100) μm , fungi 3-10(-300) μm , and ferns 30-100 μm . Crum (2001) gives a broader range from 5 (*Dawsonia*; Figure 10) to 310 (*Archidium*; Figure 22) μm , but few are greater than 30 μm . The generalization still holds that those taxa that produce small spores produce lots of them and those with large spores produce few (Schuster 1984) (50 million in *Dawsonia*, 4 in *Archidium*; Table 2).

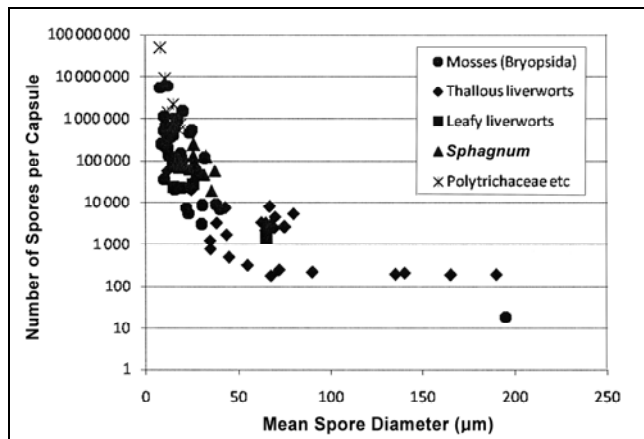


Figure 64. Inverse relationship of number of spores produced per capsule to spore size. Redrawn from Lönnell 2011.

Large Spores

Archidium (Figure 22), as a genus, sets the record for spores size in mosses. This larger size permits it to maintain a large food reserve that becomes available when the moss germinates. In its open habitat, this permits it to develop quickly and complete its life cycle before conditions once again become unfavorable for growth. *Archidium brevinerve* has the largest average spore diameter (235 μm); *A. ohioense* (Figure 65) has the largest measured spore (310 μm) (Snider 1975). In Europe the most widespread species in the genus is *A. alternifolium* (Figure 22) with an average spore size of 162 μm and range of 139-223 μm (Boros *et al.* 1993). Among the liverworts, *Asterella* has spores 135-160 μm in diameter (Figure 66). *Sphaerocarpos* (Figure 67-Figure 68) sheds its spores in tetrads, making those spore dispersal units quite large. They furthermore are highly decorated, creating air spaces that could increase surface area without adding weight and increasing floatability. Some spores are **precocious** (Figure 71), *i.e.*, germinating within the spore wall and typically before leaving the capsule. Such spores are consequently larger and presumably heavier, as for example those of *Tuyamaella molischii* (Lejeuneaceae; Figure 69-Figure 71) that are up to 140 μm long (Rui-Liang Zhu, Bryonet 6 March 2013).



Figure 65. *Archidium ohioense* with sporophytes. Photo by Li Zhang, with permission.

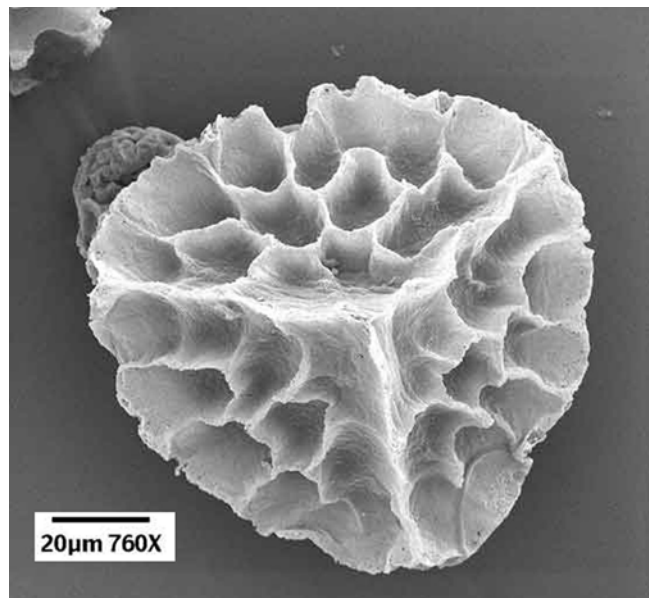


Figure 66. *Asterella bolanderi* spore proximal view SEM. Photo by William T. Doyle, with permission.



Figure 67. *Sphaerocarpos michelii*. Photo by Jan-Peter Frahm, with permission.

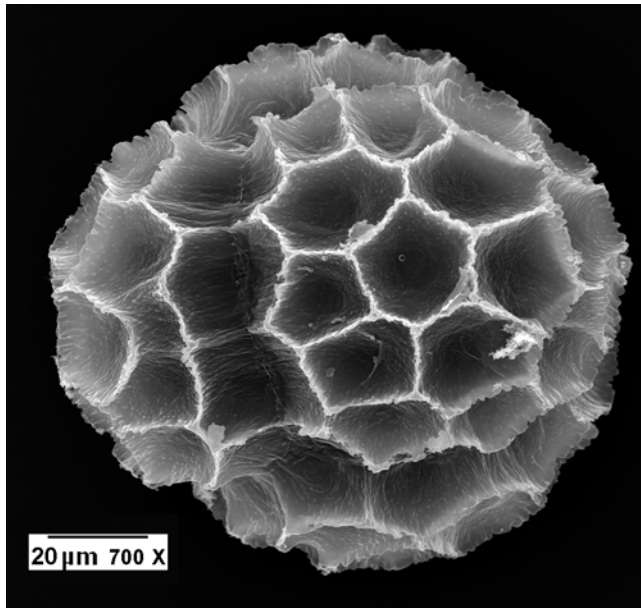


Figure 68. *Sphaerocarpos texanus* spore SEM, showing highly decorated wall. Photo courtesy of Karen Renzaglia.

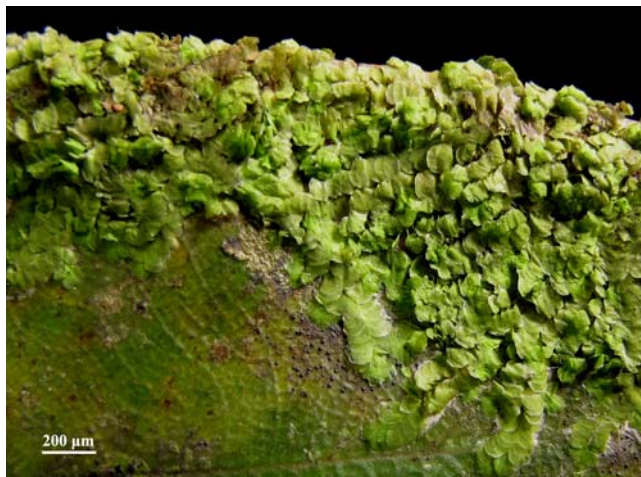


Figure 69. *Tuyamaella molischii* var. *molischii*, an epiphyllous liverwort from Guangxi Pinglongshan, China. Photo by Rui-Liang Zhu, with permission.



Figure 70. *Tuyamaella molischii* var. *molischii* capsules from Guangxi Pinglongshan, China. Photo by Rui-Liang Zhu, with permission.

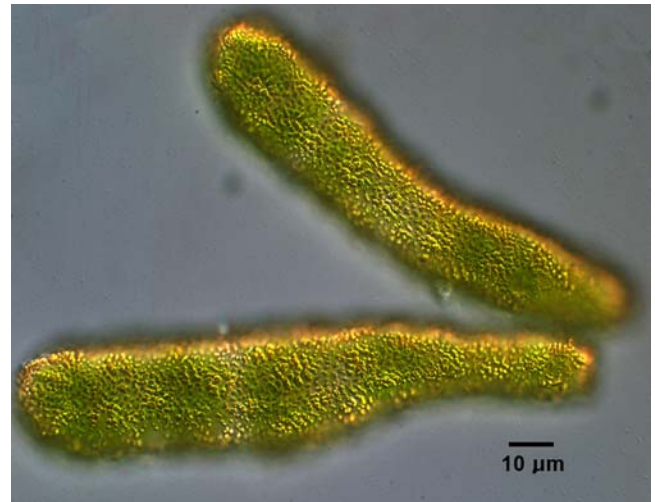


Figure 71. *Tuyamaella molischii* var. *molischii* precocious spore development, from Guangxi Pinglongshan, China. Photo by Rui-Liang Zhu, with permission.

In *Archidium alternifolium* (Figure 22), little or no protonema develops when the spore germinates (Miles & Longton 1992a). Rather, a germling shoot arises from the dehiscing spore(!), or shortly thereafter from a short protonema. This ability most likely arises through the complements of an adequate food supply in the large spore, precluding the need for a protonema to store such energy before a shoot can be formed. But other factors might also be at play. Could it be that necessary hormones to stimulate the shoot growth are carried in this large spore, sacrificed in small spores to make room for the little bit of nutrient matter it can provide? Such hormones, in the case of small spores, might then be provided by the protonema, or in the surrounding environment (see discussion on Delayed Germination in subchapter 4-7).

It appears that the large size of the spore in *Archidium alternifolium* (Figure 22) might afford other advantages as well. When Miles and Longton (1992a) cultivated the spores on agar, germination spanned a period of several months. Furthermore, the spores remained viable for up to four years following field collection of fresh material. But it is interesting that in the field these spores seem to lack what it takes for any dispersal. Rather, they remain in the capsule, attached to their parent plants. Despite the spore longevity and size, according to Miles and Longton, it is the fragments that predominate in the diaspore bank and form the recolonizing population following disturbance.

Convey and Lewis Smith (1993) suggested that large spore sizes observed in short-lived species may be important in local colonization in the Antarctic. Those taxa that are annual or short-lived invest more in spore dispersal than those in most perennial taxa. Nevertheless, on Signy Island in the Antarctic, spore size did not seem to influence dispersal potential in the five taxa identified (Marshall & Convey 1997).

For whatever reason, acrocarpous spores of Michigan, USA, mosses are generally smaller (mostly <25 μm in diameter) than those of pleurocarpous taxa (mostly >25 μm), based on sizes provided by Crum (1973). These evolutionary trends may not relate to habitat, but we do know that pleurocarpous mosses are perennial and rely less on spores for their reproduction than do many of the

acrocarpous taxa. Having larger spores provides more energy for a better start in life. Liverwort taxa may have a similar division between leafy and thallose taxa, if Schuster's table (Table 3) on spore size is any indication, but the number of taxa represented is far too small to draw any generalizations.

Table 3. Spore size (µm) in liverworts. The first six are leafy. Based on Schuster (1966).

<i>Scapania</i> (=Diplophyllum) <i>albicans</i>	10-14
Blepharostomaceae	8-16
<i>Chiloscyphus</i> (=Lophocolea) <i>cuspidata</i>	14-16
<i>Scapania undulata</i>	15-20
<i>Sendtnera</i> (=Herbertus) <i>adunca</i>	25
Ptilidiinae	15-65
<hr/>	
<i>Sphaerocarpos michelii</i>	30-40
<i>Pellia epiphylla</i>	50-60
<i>Sauteria alpina</i>	60-70
<i>Preissia quadrata</i>	60-75
<i>Ricciella</i> (=Riccia) <i>crystallina</i>	65-80
<i>Reboulia hemisphaerica</i>	60-90
<i>Conocephalum conicum</i>	70-90
<i>Riccia glauca</i>	80-100
<i>Riccia gougetiana</i>	180-200

The number of spores per meter square is a function not only of the number of spores per capsule, but also the density of the capsules present. Some of these numbers are enormous (Table 4).

As already noted, spore number is determined not only by the number per capsule, but also by the number of capsules produced. More capsules can correlate with wider dispersal and wider distribution. Robinson (1990) pointed out this relationship in the **Leucobryaceae**, where ***Octoblepharum albidum*** (Figure 72) typically has many sporophytes and has one of the widest distributions in the family. In many genera in this family, sporophytes are reduced, but propagation by leaves and leaf fragments is common. Robinson suggests that birds and other arboreal animals could facilitate dispersal among the epiphytic members of the family.

Spore size is an integral part of life history strategies. Longton (1988) summarized some of these relationships for arid regions. He found that perennial stayers are typically acrocarpous mosses with small spores, long spores, and "other features promoting dispersal." Annual shuttle species, conversely, produce large spores, often in submersed capsules, promoting rapid germination and establishment *in situ*, but not well adapted for dispersal. Perennial shuttle species are mostly marchantialian liverworts with large spores. Fugitives stay at a given site and are able to do this by having small, easily dispersed spores.

Jenkins *et al.* (2007) attempted to use existing data from many data sets to answer the question of size vs dispersal distance. They divided organisms into active and passive dispersers, defining active dispersers as those that arrived at a new location under self-propulsion. This includes most vertebrates and arthropods, but many other animals depend primarily on passive sources. Plants, including bryophytes, are mostly passive dispersers.

Jenkins and coworkers found that active dispersers, as expected, dispersed significantly farther and were significantly greater in size ($P<0.001$). Passive dispersers, on the other hand, had random dispersal distances compared to mass/size. They concluded that while size is important for active dispersers, it is not for passive dispersers. But could there still be a relationship for dispersal units less than a certain size that permits them to be dispersed by air currents? Jenkins *et al.* consider that dispersal-size relationships for microbes cannot be tested by direct observation. Perhaps that for bryophytes will be somewhat easier. In their analysis for passive dispersers, Jenkins and coworkers used organisms weighing in the range of 10^{-8} to 10^{-9} g, dominated by plant seeds. This hardly seems a good model for bryophytes with single-celled spores as their dispersal agents.

Table 4. Number of bryophyte spores per m². Liverwort taxa in bold face.

<i>Anthoceros agrestis</i>	14 mil/m ²	Bisang 2001
<i>Sphagnum</i>	16 mil/m ²	Sundberg 2002
<i>Atrichum undulatum</i>	37 mil/m ²	Longton & Schuster 1983
<i>Pleurozium schreberi</i>	100 mil/m ²	Longton 1976
<i>Ptilidium pulcherrimum</i>	20-300 mil/m ²	Jonsson & Söderström 1988
<i>Grimmia pulvinata</i>	7,400 mil/m ²	Longton & Schuster 1983
<i>Tortula muralis</i>	38,300 mil/m ²	Longton & Schuster 1983



Figure 72. Capsules of the epiphytic ***Octoblepharum albidum***. Photo by Janice Glime.

Spore Weight

Hughes *et al.* (1994) developed a set of provisional conclusions regarding the relationship of dispersal mode and other attributes of plants and their habitats. Although these were developed with seed plants in mind, examining them for bryophytes might be instructive in developing our own hypotheses. They concluded that seeds larger than 100 mg tend to be adapted for dispersal by vertebrates, whereas those less than 0.1 mg tend to be unassisted.

Bryophyte spore weights do not seem to have been a priority for bryologists, so it is necessary to estimate. Most spores range from 20 to 100 µm in diameter (Boros *et al.*

1993). A 20 μm spore has a radius of 10 μm . Knowing that, we can calculate its weight by assuming it is a sphere, starting by determining the volume ($V = 4/3 \pi r^3$). Hence, the volume would be $4.188 \times 1000 = 4188$ cubic microns. Assuming that a spore is mostly water, and knowing that the weight of water is 1000 g per liter, a cubic micron is 10^{-15} L or 10^{-9} μL . Hence, 1 cubic micron weighs 10^{-12} grams or 10^{-3} nanograms. A 20 μm spore would weigh only 4.2×10^{-9} g (0.0042 μg , or 4.2 nanograms) when fully hydrated ($V = 4/3 \pi r^3 = 4188$ cubic μm ; 1 cubic $\mu\text{m} = 10^{-9}$ μL ; 1 $\mu\text{L} = 1$ μg of water; 1 μg weighs 1 million picograms). Using a sphere as our model, we can derive the formula:

$$\begin{aligned} \text{spore weight} &= 4/3 \pi r^3 (10^{-3}) \text{ nanograms} \\ \text{or} \\ \text{spore weight} &= 4/3 \pi r^3 (10^{-6}) \mu\text{g} \end{aligned}$$

It is rather easy to do this calculation at <http://www.wolframalpha.com> and inserting "weight of sphere of water 20 microns in diameter."

Spores that are 100 μm in diameter would weigh 0.524 μg and often travel only downward by gravity, as in *Archidium* (Figure 22). Since bryophyte spores therefore fall in the less than 0.1 mg category, they support the hypothesis of Hughes *et al.* (1994) that diaspores less than 0.1 mg tend to be dispersed unassisted. Nearly all of the spores of bryophytes are apparently unassisted in their dispersal (*i.e.*, unassisted by animals, with only undirected wind and water for assistance).

Even at 300 μm diameter in *Archidium* (Figure 22) (Snider 1975), the spores of such bryophytes would weigh only 14.1 μg . Spores are usually dry when they travel, making them even less in weight.

The formula provides an estimate of the maximum weight of a spore with the density of water. Most spores are not fully hydrated and the spores may be slightly flattened into a tetrahedron with one rounded side. Whitaker and Edwards (2010) assumed a spore shape of a tetrahedron with a circular base to calculate the weight of a *Sphagnum* spore and determined a weight of 1.7 nanograms for a spore with a base diameter of 28 μm . If we assume that this spore is all water and spherical with a diameter of 28 μm , it would weigh 11.5 nanograms, a rather substantial difference in estimation caused not only by the shape assumption, but also by the water assumption.

Spores vary in weight between species, even at the same spore sizes. These variations depend on food reserves and water content (Jeff Duckett, Bryonet 6 March 2013). Green spores are short-lived, commonly remain hydrated, and typically store their food as starch, giving them a specific gravity greater than 1 and making them heavier than brown spores. Brown spores are generally smaller, long-lived, and use both protein and lipid reserves. They are usually very dehydrated and have a specific gravity considerably less than 1. Hence, green spores usually sink in water; brown ones usually float and, presumably, more easily become airborne.

But Gradstein (Bryonet 11 March 2013) argues that green vs non-green spores from nearly 100 tropical species do not correlate with range sizes or with long-range dispersal, based on an experimental study (van Zanten & Gradstein 1988). No differences correlated with drought or

low temperatures for exposures from a few hours to a year or more.

We can estimate weight by the size of the spore, but as noted, not all spores are created equal. The specific gravity is a more important measure of the transportability than the weight (mass) alone. Peter Poschlod (pers. comm. 6 March 2013), like Duckett, points out that some spores float on water whereas others sink. Among the ones that sink immediately are those of *Sphagnum*. Using spore traps in peatlands, Poschlod (1995) was unable to find any *Sphagnum* spores. Rather, the traps produced vegetative parts, especially those of *Sphagnum* (Figure 73). Dry *Sphagnum* is especially light weight and easily becomes airborne, as I witnessed one day while watching ants trying to repair their mound during a windstorm. In grasslands, on the other hand, vegetative diaspores tended to be the exception. Nevertheless, in the grasslands it appeared that grazing animals, especially sheep, transported the mosses, particularly ones such as *Abietinella abietina* (Figure 74) that in Central Europe does not produce capsules.



Figure 73. *Sphagnum* protonemata growing on a *Sphagnum* branch in the field. Photo by Andras Keszei, with permission.

Survival and Longevity

Some spores, under the right conditions, can survive extremely long periods (Table 5). Gubin *et al.* (2003) reported viable moss spores from permafrost sediments in northeast Eurasia, citing ages of tens to thousands of years of preservation.



Figure 74. *Abietinella abietina*, a species that seems to be transported by sheep in grasslands. Photo by Michael Lüth, with permission.

Van Zanten and Pócs (1981) surmised that spores from taxa in dry habitats had a generally greater drought resistance than those from wet habitats. Since liverworts tend to live in wetter habitats, grow where there is less air turbulence, and have larger spores, they further concluded that moss spores should be expected to travel farther.

Most spores that arrive at a given area will not have travelled terribly far. The majority will land within a few cm to a meter of the parent, but some are carried by air currents to far off places. In this longer transport, they will be subjected to high UV radiation and extremes of moisture and temperature.

Table 5. Known longevity for bryophyte spores, based mostly on Crum 2001. Liverworts are in bold face.

Lejeuneoideae	7-8 d	Gradstein 1994
<i>Cyathodium tuberosum</i>	9 mos	Tiwari 1935
<i>Conocephalum conicum</i>	<1 mo	Crum 2001
<i>Plagiochasma intermedium</i>	<1 yr	Crum 2001
<i>Blepharostoma trichophyllum</i>	1 yr	Crum 2001
<i>Polytrichastrum alpinum</i>	16 mos	Crum 2001
<i>Marchantia polymorpha</i>	<17 mos	O'Hanlon 1926
<i>Riella americana</i>	17 mos	Studhalter 1931
<i>Grimmia elatior</i>	17 mos	Crum 2001
<i>Mannia fragrans</i>	<18 mos	Inoue 1960
<i>Targionia hypophylla</i>	18 mos	O'Hanlon
<i>Grimmia muehlenbeckii</i>	18 mos	Crum 2001
<i>Physcomitrium pyriforme</i>	2 yrs	Meyer 1941
<i>Preissia commutata</i>	>2 yrs	Teodoresco 1929
<i>Anomodon longifolius</i>	29 mos	Crum 2001
<i>Sphagnum</i>	3 yrs	Chaloud 1932
<i>Riella paulsenii</i>	3 yrs	Porsild 1902
<i>Brachythecium velutinum</i>	1.5-4 yrs	Herguido & Ron 1990
<i>Blindia acuta</i>	4 yrs	Crum 2001
<i>Microbryum starckeanum</i>	4.75 yrs	Lesage 1918
<i>Bucklandiella (=Racomitrium sudeticum)</i>	7 yrs	Crum 2001
<i>Dicranoweisia cirrata</i>	9 yrs	Malta 1922
<i>Funaria hygrometrica</i>	11 yrs	Hoffman 1970
<i>Riella capensis</i>	13 yrs	Studhalter 1931
<i>Riella affinis</i>	16 yrs	Tenge 1959
<i>Ceratodon purpureus</i>	16 yrs	Chaloud 1932
<i>Anoetangium aestivum</i>	19 yrs	Malta 1922
<i>Oedipodium</i>	20 yrs	Chaloud 1932
<i>Dicranella</i>	50 yrs	Chaloud 1932
<i>Ricciocarpos natans</i>	50 yrs	Conrad 1996

Sphagnum in experiments suggest that *Sphagnum* spores may have a half-life of 1-20 years, but that individual spores may survive for several decades and possibly even centuries (Sundberg & Rydin 2000). Refrigerated spores retained 15-35% viability for 13 years.

Some of the records of spore longevity from herbarium specimens have been suspect due to the possibility for contamination. However, Bristol (1916) reported germination of spores and development of protonemata from spores that had been collected from the top 24 cm of soil in Great Britain 49 years earlier and stored in bottles.

Egunyomi (1979) tested the germination success of tropical moss spores that had been stored at room temperature for various periods of time from 1-3.5 years. Of the 22 species tested, 15 failed to germinate at all. Five species had better than 50% germination. He chose four of these (*Microcampylopus nanus*, *Weissia papillosa*, *Mittenothamnium overlaetii*, *Weisiopsis nigeriana*) that

had been stored at least two years for further experimentation of extreme conditions for 4 weeks: -2°C, 8°C, continuous immersion in water at room temperature, alternate wetting and air drying every 24 hours. None of the species at -2°C survived for 4 weeks. At 8°C, all survived four weeks, with survival percentages ranging 43-81%. Continuous immersion, like the -2°C, resulted in 0% survival after 4 weeks, but alternate wetting and air drying resulted a range of 45-76% survival with the success ranks by species being the same as in the 8°C treatment.

Atmospheric Conditions – UV and Desiccation

It is likely that conditions that favor the dispersal of protozoa and algae also favor the dispersal of bryophyte spores. Hence, we might expect cloudy or overcast skies to help filter UV light (Schlichting 1961). Fires and volcanoes can put particulates in the atmosphere, likewise serving as UV filters. Clouds also can prevent severe desiccation.

Drought Tolerance

Drought tolerance has the greatest correlation with transoceanic distribution (van Zanten & Gradstein 1988). Van Zanten and Gradstein found that only 5% of the transoceanic species had lost the ability to germinate after five days (the minimum time calculated for crossing the Atlantic), whereas 32% of the endemic species exhibited that limitation. Among the transoceanic species, half were able to germinate after 70 days, whereas among the endemic species only half could still germinate after 25 days. Six transoceanic species could still germinate after 100 days of desiccation: *Anastrophyllum auritum* (60% germination), *Andrewsianthus jamesonii* (50%), *Gymnocoleopsis multiflora* (50%), *Herbertus subdentatus* (Figure 75) (40%), *Dumortiera hirsuta* (Figure 76) (10%), and *Chiloscyphus* (as *Lophocolea*) *muricata* (Figure 77) (5%). Some even lasted 150 days. Nevertheless, three endemic species germinated after 100 days of desiccation: *Cephalozia crassifolia* (Figure 78) (10%), *Marchantia chenopoda* (Figure 79-Figure 80) (80%), and *Fossombronina* sp. (Figure 81) (80%), with the latter species even germinating after 150 days. These three endemic taxa have large, dark-colored spores, suggesting they could also survive UV light, but van Zanten and Gradstein suggest that these are probably adaptations for surviving adverse climatic periods, not long-distance dispersal.



Figure 75. *Herbertus subdentatus*, a species with 40% germination after 100 days desiccation. Photo by Michael Luth, with permission.



Figure 76. *Dumortiera hirsuta* thallus with archegoniophore, a species whose spores had 10% survival of desiccation for 100 days. Photo by George Shepherd, through Creative Commons.



Figure 77. *Chiloscypus muricatus*, a species whose spores had 5% survival of desiccation for 100 days. Photo by Andrew Hodgson, with permission.

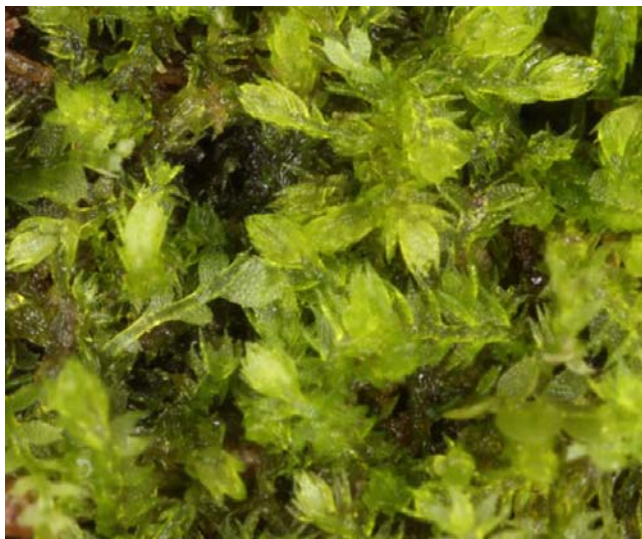


Figure 78. *Cephalozia crassifolia*, an endemic species whose spores had 10% survival of desiccation for 100 days. Photo by Jan-Peter Frahm, with permission.

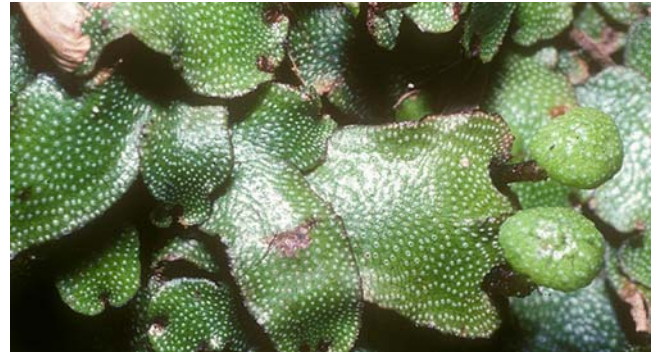


Figure 79. Thallus and antheridiophores of *Marchantia chenopoda*, an endemic species whose spores had 80% survival of desiccation for 100 days. Photo by Janice Glime.



Figure 80. *Marchantia chenopoda* with archegoniophore and gemma cups. Photo by Janice Glime.



Figure 81. *Fossombronia japonica*, genus with an endemic species whose spores had 80% survival of desiccation for 100 days. Photo by Li Zhang, with permission.

The liverwort *Gymnocoleopsis multiflora* has unusual spores that are very durable despite thin spore walls and hygrophytic habit (van Zanten & Gradstein 1988). Both spores and sporelings are fairly resistant to UV radiation, as well as being very durable. These appear to be adapted to the high alpine habitat where it lives. By contrast, *Riccardia amazonica* and *Stictolejeunea balfourii* live in the understory of wet primary rainforest and their spores have very poor drought resistance. Such examples suggest that the spore adaptations may be more related to the habitats of the parents than to dispersal capabilities. In fact, most of the transoceanic species van Zanten and Gradstein tested came from more open habitats such as forest margins – habitats that would require more of the

same habitat adaptations as long-distance space travel, and where getting into the airstream may be easier than in the forest.

Frost Resistance

Van Zanten and Gradstein (1988) found that spores of transoceanic species had significantly better frost tolerance than endemic species, especially among spores that were desiccated for one week before the freezing treatment. Those spores that had been dried had better resistance in small-spored species than in large-spored ones, suggesting again that small-spored species should travel farther.

Nevertheless, wet freezing does not seem to favor the transoceanic species more than the endemic species (van Zanten & Gradstein 1988). Hence, it is not likely to affect the dispersability of liverworts. Interestingly, fresh spores are less likely to survive dry freezing, and this danger is more pronounced in the endemic species.

UV Protection

The greatest danger, considered by van Zanten (1976) and van Zanten and Gradstein (1988), is that of UV radiation damage. This poses a special problem because dry conditions that make them light in weight are also usually sunny conditions. Schlichting (1961) considered the greater success of UV-sensitive organisms (algae and protozoa) under humid and cloudy conditions to be due to the diminished impact of UV radiation, a concept supported by van Zanten and Gradstein. The added moisture also counteracts the severe desiccation often experienced in the upper atmosphere. The fact that algae have been collected by aircraft from 2000 m above the Earth suggests that bryophyte diaspores likewise occur there. Schlichting (1958) even reported viable moss spores from fingerbowls exposed at 2 m above the ground over periods of 45 minutes to 32 hours.

But we also know that UV light is used to kill cells, and bryophyte spores are no exception. Van Zanten and Gradstein (1988) tested the effects of UV radiation on spores in nearly 100 tropical liverwort species by flying them from Amsterdam to Los Angeles on the wings of a commercial 747 jet. Only two species, both from above 3000 m asl in the Andes, survived the journey, suggesting that the jet stream is not an available avenue to most species, at least among liverworts. This greater resistance to UV damage displayed by high altitude species may explain the distribution of species along mountains – perhaps a better explanation than the flyway explanation. But the two aspects could work together. In short, most species seem to be unable to survive the dosage of UV radiation required for long-distance dispersal under most conditions.

Some spores travel with chlorophyll. But van Zanten and Gradstein (1988) found no correlation between chlorophyll presence and species range. Furthermore, they found no relationship between precocious germination and local dispersal or between non-green and long-distance dispersal. There also seemed to be no dormancy effect.

Some spores have dark pigments; others have cuticular ridges or other extrusions, including papillae. It would be interesting to correlate those characters with success of the spores in travelling long distances where they must survive the greater desiccation and UV light of the atmosphere.

We need to understand just what levels of UV are present under dispersal conditions, what levels kill spores and other diaspores, and how long the exposure must last to cause damage. On the other side, we need to understand what characteristics of spores protect them from this damage, how moisture affects that damage potential, and is there a set of conditions and adaptations that would permit long-distance dispersal.

Liverwort Spore Survival

Fulford (1955 in Schuster 1966) considered that spore survival of leafy liverworts was short, but she actually had only one citation (Figure 82; Bernstein 1928) – for one species (*Blepharostoma* sp; Figure 83) – to back up this assumption; since then we have learned that some have considerable longevity. Inoue (1960) tested spore longevity in six liverwort taxa (Table 6) and found survival up to 18 months in three of them. Malta (1922) failed to obtain germination of spores from *Plagiochila asplenoides* (Figure 84) or *Pellia epiphylla* (Figure 85-Figure 86) after four years or of *Preissia quadrata* (Figure 87) after eight years of storage. Nevertheless, as van Zanten and Gradstein (1988) have demonstrated, those species with transoceanic distributions typically have longer viability.

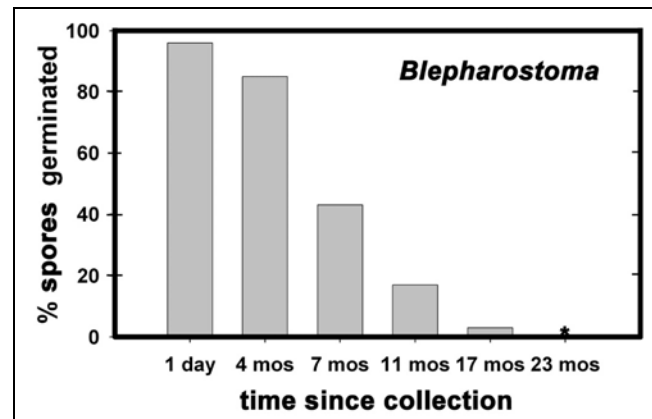


Figure 82. Decline in spore germination in *Blepharostoma* from the first day after collection onward. * refers to one spore that germinated out of 512 after 23 months. Based on data from Bernstein 1928.

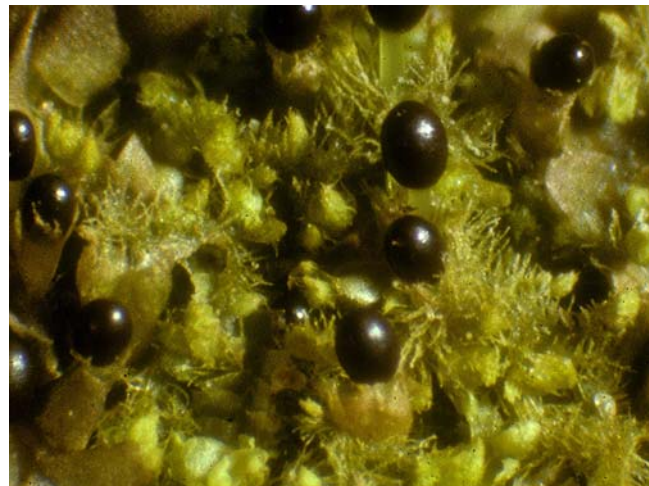


Figure 83. *Blepharostoma trichophyllum* with capsules, a species with short spore survival. Photo by Janice Glime.

Table 6. Percentage of spore viability in Marchantiales. From Inoue (1960).

	1 mo	6 mos	12 mos	18 mos
<i>Reboulia hemisphaerica</i>	100	100	95	11.3
<i>Plagiochasma intermedium</i>	-	48	0	0
<i>Mannia fragrans</i>	100	100	76	0.0
<i>Marchantia polymorpha</i>	100	100	87	43
<i>Marchantia paleacea</i>	100	100	72	21
<i>Conocephalum conicum</i>	0	0	0	0



Figure 84. *Plagiochila asplenoides*; spores failed to germinate after four years of storage. Photo by Dick Haaksma, with permission.



Figure 85. *Pellia epiphylla* with sporophytes; spores failed to germinate after four years of storage. Photo by Kristian Peters, with permission.



Figure 86. *Pellia epiphylla* spore. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.



Figure 87. *Preissia quadrata* with archegoniophores; spores failed to germinate after eight years of storage. Photo by Janice Glime.

Schuster (1983) has suggested that many liverworts that survive as relict populations are limited in their dispersal success by being dioicous, being unable to withstand desiccation, and lacking asexual reproductive structures. He suggested further that successful dispersal can be enhanced by 1) formation of sexual propagules (*Lophozia-Scapania* model), 2) production of large numbers of very small spores per sporophyte (numerically overwhelming), 3) dispersal of spores mixed as monads, diads, and tetrads (*Haplomitrium* model) (see Figure 88), 4) spores permanently united in tetrads (*Cryptothallus-Sphaerocarpos* model), 5) acquisition of desiccation tolerance coupled with numerical overwhelming (xerothermophyte model), and 6) monoicicism (*Calypogeia-Isopachtes* (= *Lophozia bicrenatus-Cololejeunea* model).

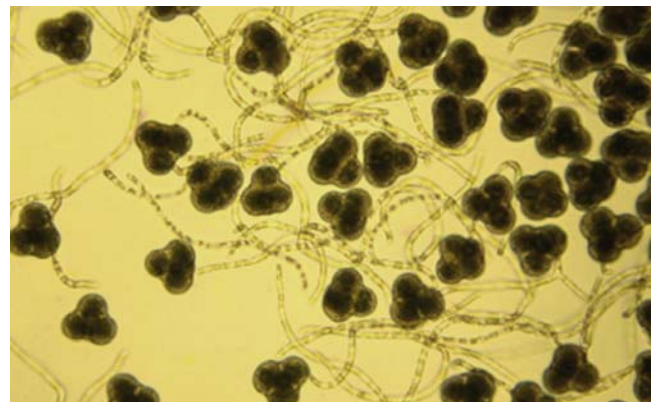


Figure 88. *Porella navicularis* spore tetrads as they appear after meiosis and before separation. From botany website, University of British Columbia, with permission.

Adaptations for Survival

Many bryophyte spores seem to be particularly endowed to survive extremes during their travels. The first evidence of this is that they have resisted decay and remain in huge numbers in deposits from the Silurian and Devonian periods. But biochemical evidence tells us more of their survival capabilities. Each spore obtains a **callose** (glucose polymer related to cellulose) deposit before the **exine** (outer layer of spore) completely forms (Crum 2001). Then the exine attains a **polysaccharide** deposit impregnated with **sporopollenin** (that waxy substance similar to cutin that covers pollen). Last, the **intine** develops with cellulose and other polysaccharides. Once

the formation of the wall is complete, **Takakiopsida**, **Sphagnopsida**, **Andreaeopsida**, and **Bryopsida** spores deposit a **perine** layer that creates ornamentation. As Crum (2001) describes it, this layer is the "detritus" from the walls of the spore mother cells and remains of the columella. Thus, liverworts and hornworts, lacking a columella, also lack the perine deposit. It is the sporopollenin layer that affords all these spores their resistance to water and decay (Crum 2001).

There is considerable documentation that under the right conditions, some spores can survive for considerable periods. Green spores, typical of species that occur in moist habitats, have a shorter viability due to their higher metabolic rate (Crum 2001). Green spores store starch as their food reserve, but yellow spores, those of longer viability, typically store oils and these species are common in drier habitats. Marin (1981) reported that among 120 species of mosses, green spores were more common (87%) than non-green spores. All epiphytic mosses had green spores, whereas non-green spores occurred in taxa of drier or disturbed soils and rocks. Some taxa use protein for their food reserves [the liverwort *Blasia* (Figure 89-Figure 90) and hornworts], but this form seems to be slower to metabolize and cannot be used for quick growth (Crum 2001).



Figure 89. *Blasia pusilla* from Europe, a species that stores its food reserves as protein. Photo by Michael Lüth, with permission.



Figure 90. Open capsule of *Blasia pusilla* showing spores and claters. Photo by Walter Obermayer, with permission.

Sundberg and Rydin (2000) found that buried *Sphagnum* spores could survive at least three years at various depths in peat. Curiously, light-colored spores of *S. balticum* (Figure 91) and *S. tenellum* (Figure 92) had higher survivorship than the darker spores of *S. fuscum* (Figure 44) and *S. lindbergii* (Figure 93), suggesting possible differences in stored food reserves. Spore size did not seem to influence longevity between species, but within a single species (*S. balticum*, *S. tenellum*) the small spores from small capsules seemed to have a greater longevity than those from medium-sized and larger capsules, something that seems counter-intuitive.



Figure 91. *Sphagnum balticum* with capsules in southern Europe. Photo by Michael Lüth, with permission.



Figure 92. *Sphagnum tenellum* with capsules, a species where spores from smaller capsules survive longer. Photo by Dick Haaksma, with permission.



Figure 93. *Sphagnum lindbergii* with capsules, a species with dark-colored spores that survive shorter periods than light-colored spores of accompanying species. Photo by Michael Lüth, with permission.

Survival in Water

Waterways offer a means of rapid dispersal. In streams they can carry diaspores great distances. In flood plains (Figure 94), diaspores can be buried in mud or travel with a river, germinating at some later point in time when they somehow reach the surface. Spores and gemmae require light to germinate, permitting these diaspores to remain dormant as long as their energy stores permit and their ability to fend off other organisms that might use them for a food source (bacteria, fungi, small animals).



Figure 94. Eroded material transported by water to River Baihe, a tributary of Yellow River Tibet. Such flood plains can house dormant bryophyte diaspores that are ready to grow when the water recedes. Photo by Sven Bjork, with permission.

To test the viability of spores and fragments of bryophytes from various habitats, Dalen and Söderström (1999) stored sets of these from *Ceratodon purpureus* (Figure 27), *Codriophorus* (= *Racomitrium*) *aciculare* (Figure 95), *Dicranoweisia crispula* (Figure 96), *Oligotrichum hercynicum* (Figure 97), and *Schistidium rivulare* (Figure 98), and for six months in water or dry. All species except *S. rivulare* exhibited reduced spore germination frequencies at all time intervals when stored in water compared to stored dry. *Schistidium rivulare*, a species that includes rocks in the splash of rivers and streams, demonstrated longer spore survival than did the other species. This species also had the highest regeneration frequencies from fragments. Nevertheless, diaspores of all these species survived at least some time in the water. In all species, the regeneration frequencies of fragments tended to be lower than those of spores. On the other hand, fragments did not experience any reduction in survival when stored in water compared to stored dry.



Figure 95. *Codriophorus* (formerly *Racomitrium*) *aciculare* with capsules, a species whose spores survive a short time in water. Photo by Jan-Peter Frahm, with permission.



Figure 96. *Dicranoweisia crispula* with capsules, a species whose spores survive a short time in water. Photo by Jan-Peter Frahm, with permission.



Figure 97. *Oligotrichum hercynicum* with capsules from southern Europe, a species whose spores survive a short time in water. Photo by Michael Lüth, with permission.



Figure 98. *Schistidium rivulare* with sporophyte, a species whose spores and fragments survive well in water. Photo courtesy of Betsy St. Pierre.

Survival of Spores vs Asexual Diaspores

Egunyomi (1978) compared viability of spores with that of gemmae in *Octoblepharum albidum* (Figure 72, Figure 99). He found that spores retain high viability for more than 8 months at temperatures of 22-30°C, 60-75% humidity, whereas gemmae lose viability at about 6 months under those conditions. Germination did not occur in darkness, suggesting that the propagules would not germinate within a diaspore bank. Nevertheless, some germination occurred in as little as 1 lux, suggesting that the species might be able to germinate among a heavy plant cover, but the question remains whether it could grow enough to survive and thrive there. Furthermore, if spores or gemmae were exposed to light, then cultured in dark, a light intensity of 800 lux for 48 & 36 hrs respectively was necessary for them to germinate at all.



Figure 99. *Octoblepharum albidum* gemmae. Gemmae of this species survive for a shorter period than do the spores at temperatures of 22-30°C and 60-75%. Photo by Li Zhang, with permission.

Germination of spores from herbarium specimens suggest that weedy species may remain viable longer than other taxa. *Ceratodon purpureus* (Figure 27) spores were the oldest to germinate – after 16 years (Malta 1922) – but this species surprisingly does not appear in the diaspore bank (Lönnell 2011). Most of the spores in the study by Malta did not germinate if they were more than 10 years old, and the greatest number were viable for only 5 years. In fact, within only 50 days of dry storage, a 30-40% loss in viability can occur (Löbel 2009). But perhaps it is the unnatural storage conditions of a lab or herbarium that causes such loss of viability. For *Sphagnum* spores, 15-35% survived 13 years of storage in humid, refrigerated conditions (Sundberg & Rydin 2000). On the other hand, tubers of *Anisothecium* (= *Dicranella*) *staphylinum* (Figure 100) remained viable for 50 years of storage (Whitehouse 1984). Keever (1957) found that herbarium specimens of *Grimmia laevigata* (Figure 101) still had 20% viability after ten years. Malta (1922) found survival of 19 years in plants of *Anoetangium aestivum* (Figure 102) and Maheu

(1922) found protonemal growth from plants of *Syntrichia ruralis* (Figure 24) after 14 years of storage.



Figure 100. *Anisothecium* (= *Dicranella*) *staphylinum* in Europe, a species whose tubers remained viable for 50 years of storage. Photo by Michael Lüth, with permission.



Figure 101. *Grimmia laevigata* with capsules in southern Europe, a species whose plants retained 20% viability after ten years of storage. Photo by Michael Lüth, with permission.



Figure 102. *Anoetangium aestivum* from Europe, a species whose plants survived for 19 years in a herbarium. Photo by Michael Lüth, with permission.

Species from flood plains and other disturbed habitats may have some of the longest dispersal times. They may have considerable distances to traverse to reach a new location, and they may have long periods of unsuitable habitat requiring long survival. *Riccia* provides a good example of such a need. Breuil-Sée (1993) found that specimens of *Riccia macrocarpa* from Tunisia survived in a dry state in the herbarium for more than 23 years. Within three days of rehydration they exhibited new cells at the apices.

Long-distance Survival

Van Zanten, in his numerous papers on dispersal (1975, 1976, 1977a, b, 1978a, b, 1983, 1984, 1985, van Zanten & Gradstein 1987, 1988, van Zanten & Pócs 1981), has shown the possibilities for long-range dispersal based on experimental evidence of survival. Van Zanten (in Gradstein & Pócs 1989) showed that New Zealand **endemics** (growing only in that area) had less resistant spores than those of wide-ranging taxa and that spores of tropical moss species, especially lowland rainforest taxa, are less resistant to drought than are temperate taxa, but surprisingly, the tropical taxa survive wet-freezing at -30°C! Tropical liverworts had similar relationships, but in general were less viable under extreme conditions than were the mosses (Van Zanten & Gradstein 1987). Trans-oceanic liverworts from Colombia have better resistance to desiccation and wet-freezing than endemic taxa. Nevertheless, only spores of *Marchantia chenopoda* (Figure 79), of the 61 species tested, survived travel on the wing-tips of an airplane. But death rates were also very high for the spores transported inside the wing. Van Zanten and Gradstein concluded that jet-stream altitudes were not favorable to long-distance dispersal, but that travel in wet air currents at high altitudes was a possibility for most of these liverworts. Dry air currents were more lethal.

Van Zanten (1977b, 1978b) found one puzzling relationship in longevity. After testing survival of drought, dry freezing, and wet freezing (up to 3 years), he found that spores from Northern Hemisphere bryophyte species tended to have a longer viability than those from the Southern Hemisphere. Not surprisingly, species with restricted distributions tended to have shorter periods of viability than species that occurred on multiple continents.

It appears that some spores, perhaps even the majority, can survive for many years provided they remain dry and in the dark. A false start in which they become hydrated and begin germination can be fatal if they are not permitted to continue development and produce sugars photosynthetically.

Establishment Success

As Brent Mishler pointed out on Bryonet (6 March 2013), particulate matter from China commonly reaches California. Dust from the Sahara reaches Texas. The opportunities for worldwide dispersal seem sufficiently common that most bryophytes should be everywhere, but "the environment selects." Once the propagules enter the transport stream, they must survive, arrive, germinate, and establish (SAGE).

Greater success of spores as a means of establishment through dispersal seems to be correlated with a lower age of first reproduction and greater phenological flexibility, but suffers a tradeoff, being correlated with decreased longevity (Longton 1997). For the conservation of rare species, the conditions of establishment upon arrival are particularly important (Cleavitt 2005). Hutsemekers *et al.* (2008) determined that rare species not only require specific habitat conditions, but that they typically are unable to compete. Therefore, when new habitats, such as slag heaps, are created, the rare species tend to enter at intermediate stages, after establishment of widespread species, but before the perennial competitors become established.

Buck (1988), in his study of the Tepui of Venezuela, hypothesized that the lack of moss flora on the summit of the Tepui was due to lack of dispersal from great distances and that available spores came from surrounding lowlands. Thus, failure of a diverse moss flora on the summit must be due to lack of adaptation for germination and survival on the summit. He was fortunate enough to be able to test this hypothesis when he discovered a "world within a world" on top of a Tepui. A sinkhole, 352 m wide and just as deep, provides a haven away from wildly fluctuating moisture and temperature conditions of the summit. In this sunken world, a forest similar to that of the lowland exists. He did indeed find that the moss flora in this sunken forest reflected that of lowland and not that of the summit, supporting his hypothesis that it was ecological conditions and not lack of dispersal that created the depauperate flora.

Germination success seems to be a major problem for spores, and much less so for vegetative propagules. Miles and Longton (1990) found no evidence of spore germination for *Polytrichum strictum* (Figure 55) in the field, but did find new shoots arising from vegetative fragments. By contrast, in *Funaria hygrometrica* (Figure 103-Figure 105), spore germination and establishment occurred frequently. Intermediate results were evident in *Atrichum undulatum* (Figure 6) and *Bryum argenteum* (Figure 7), with frequent regeneration from shoot fragments, and spores germinating, but sporelings usually failed to develop. Shoots seemed to develop easily in the latter two from protonemata planted in the field.

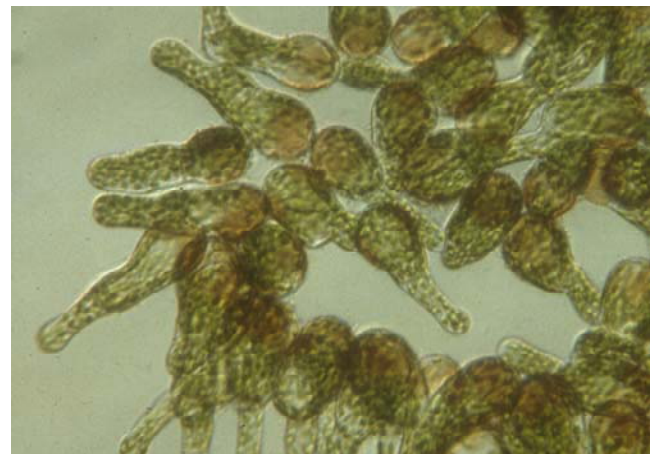


Figure 103. *Funaria hygrometrica* germinating spores on agar, demonstrating the ease of germination of many spores. Photo by Janice Glime.

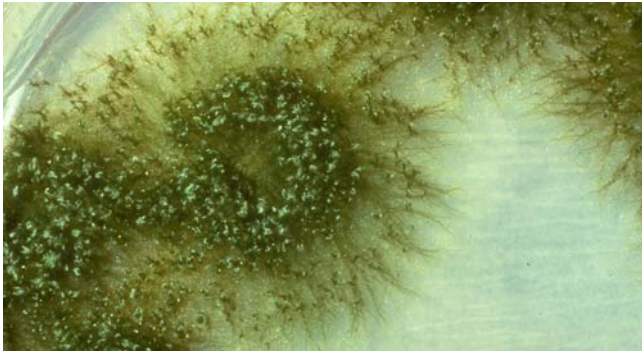


Figure 104. *Funaria hygrometrica* cultures. Each donut-shaped colony developed from a single spore, demonstrating how easily this moss can spread upon arrival. Photo by Janice Glime.



Figure 105. *Funaria hygrometrica* capsules, demonstrating the prolific production of capsules and spores. Photo by Li Zhang, with permission.

In the Negev Desert, it may be the ants in the genus *Messor* (Figure 106) that ensure the success of at least some moss spores (Loria & Herrnstadt 1980). They carry the capsules of *Crossidium crassinerve* (Figure 107) away to their nests, thus greatly increasing the likelihood that at least some spores will arrive in a suitable site for protonematal survival.



Figure 106. *Messor barbarus*, an ant that carries moss capsules, hence dispersing spores. Photo by José Miguel León Ruiz, through Creative Commons.



Figure 107. *Crossidium crassinerve* with a young sporophyte that might later be used in an ant's nest. Photo by Michael Lüth, with permission.

Spores can be a means of surviving while competitors make living conditions impossible. Newton and Mishler (1996) found evidence of inhibition by mature plants on the germination of spores. However, if something were to destroy those mature plants, the sporebank could provide a new source of propagules for re-establishment. In fact, it appears that mature plants can have a sneaky way of prolonging time until germination of their spores. Mishler and Newton (1988) found that germination rates of both *Dicranum* (Figure 108) and *Tortula* (Figure 109) were greatly lowered on substrates of their parents. Although both *Dicranum* (Figure 94) and *Tortula* were severely affected by the presence of their parents, fragments were less affected than spores. *Dicranum* had an even greater inhibitory effect than did *Tortula*. Mishler and Newton compared this to the inhibitory effect that female *Dicranum scoparium* (Figure 108) has on spores that produce dwarf males when they germinate on the female plants. Mishler and Newton (1988) found that spores did better in continuously hydrated conditions, whereas fragments fared better when they had occasional drying.



Figure 108. *Dicranum scoparium* on the forest floor where it grows dwarf males on its own leaves. Photo by Janice Glime.



Figure 109. *Tortula muralis*, a species that has poor germination in company of its parents. Photo by Kruczy89, through Creative Commons.

Keever (1957) found that spore germination of *Grimmia laevigata* (Figure 101) does occur on granite rock, but even there, fragments were more successful. One factor that influences the success of fragments vs spores is state of hydration, and this may have played a role in the establishment of *Grimmia laevigata*.

Hedderson (1992) found that rare mosses in the Terra Nova National Park, Newfoundland, Canada, were typically representatives of temperate, Arctic-montane, or montane floras. They are species at the edges of their ranges. He found that dispersal potential was negatively associated with rarity. These species have a narrow range of habitats and therefore are likely to have establishment problems.

Adherence

Arrival on the proper substrate is pretty much the end of the transport part of the story for most substrata, but for epiphytes and bryophytes on other vertical surfaces, or for those in flowing water, the problems don't end there. They must next adhere so that wind and rain don't take them once again on their journey. Van Zanten and Gradstein (1988) found that for Neotropical liverworts, the spore surface of epiphytes typically had finely verrucose spores with rosettes of large papillae (Figure 110). They suggested that these decorations were an adaptation that permitted them to adhere to rough surfaces such as bark. Epiphyllous and desert taxa, on the other hand, typically have spores that lack these rosettes (Figure 111). Both groups may gain further advantage by having precocious spore germination (Figure 71), permitting them to continue growth upon landing and gain a wider surface of adhesion.

Adherence may also be a problem in some aquatic habitats, such as streams and flood plains. But here the relationship is not so clear. Spores of *Riella* (Figure 112) are clearly spiny, possibly permitting them to adhere to the substrate more easily, but those of *Fontinalis* (Figure 113), a genus that typically adheres to rocks or underwater roots, are nearly smooth, having only small, rounded papillae.

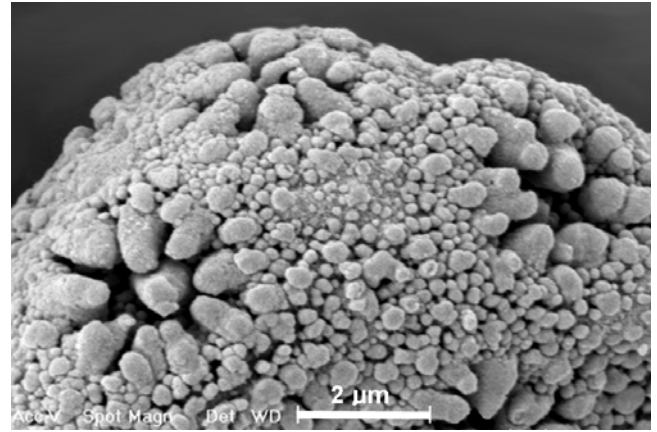


Figure 110. *Frullania chevalieri* spore SEM showing the rosettes of papillae. This spore exhibits characteristics that are common among epiphytes. Photo by Matt von Konrat, with permission.

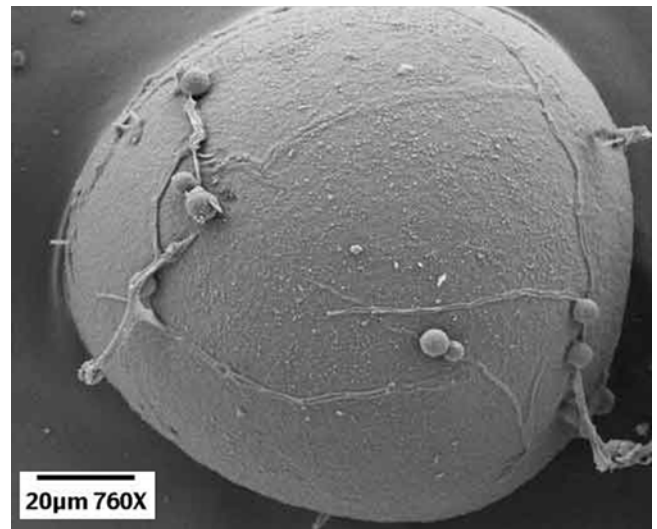


Figure 111. *Geothallus tuberosus* (Sphaerocarpaceae) spore SEM, a species of hot deserts. The large size and smooth surface are typical of spores that don't travel far and don't have adherence problems on their landing surfaces. Photo by William T. Doyle, with permission.

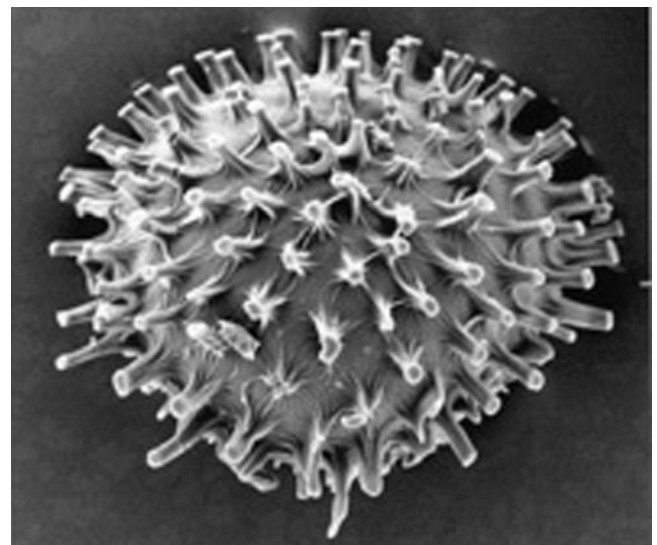


Figure 112. *Riella americana* spore SEM. Photo by William T. Doyle, with permission.

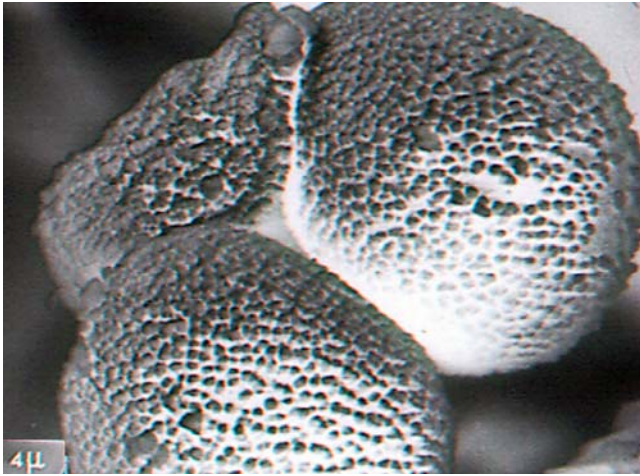


Figure 113. *Fontinalis squamosa* spore tetrad SEM. Photo by Janice Glime.

Conditions Matter

It is clear that survival while getting there is only part of the battle. Although the spores may arrive in viable condition, they may not succeed in germinating. Hassel and Söderström (1999) collected spores from *Pogonatum dentatum* (Figure 114) and germinated them in the laboratory. They had 96.6% germination within 21 days. They tested success in the field by sewing spores from 0.5, 1, and 2 capsules on 37 replicate quadrats of 10x10 cm. Considering the large estimated number of spores per capsule of 712,000, germination success was abysmal, with means of 11, 10, and 12 shoots produced, respectively, in the first year. They suggested that they had exceeded maximum density for successful protonemata. But it could also mean that some other field condition was not conducive to protonema development.

During (1986) found a similar problem in *Funaria hygrometrica* (Figure 103-Figure 105). In the greenhouse, shoots emerged from chalk grassland soil samples, even after two years, but in the field, none emerged. During considered that this failure in the field might be due to insufficient water or nutrients.



Figure 114. *Pogonatum dentatum* in Norway. Photo by Michael Lüth, with permission.

Drought tolerance of liverwort sporelings is significantly different between transoceanic and endemic species. This is a critical period for many species, with 30% of transoceanic species germinating after 50 days of desiccation and 30% of endemic species reduced to 30% germination after only 13 days. Both groups have a sporeling longevity of only about half that of spore longevity.

The problem of crowding, as suggested by Hassel and Söderström (1999) for *Pogonatum dentatum* (Figure 114), is only one problem faced by germinating spores close to the parent, and is one of little significance for long distance dispersal. The low numbers are more likely due to other problems in the field as well, including perhaps too much UV light, insufficient nutrients or moisture, or unsuitable temperatures. Noguchi and Miyata (1957) pointed out that at least some mosses with wide geographic ranges have abundant spores but are confined in their frequency by having rather specific habitats.

Multiple factors contribute to the success of a species upon its arrival. The conditions required for germination and development of the protonema and gametophore buds may differ, and are all part of the niche of a species, a topic that will be discussed in more detail in another volume. But it is appropriate to consider some examples here as we define limits of establishment.

Wiklund and Rydin (2004) compared spore establishment of two forest bryophytes, one [*Neckera pennata* (Figure 15-Figure 16)] an epiphyte and the other [*Buxbaumia viridis* (Figure 115)] an inhabitant of decaying logs. Using *in vitro* experiments, they determined that *Neckera pennata* was less successful at germinating at a low pH than was *Buxbaumia viridis*. The tradeoff was that *N. pennata* exhibited earlier germination at low water potential and survived longer when desiccated. They suggested that the higher pH would speed up germination and enable the spores to exploit short moist periods. This niche separation at the time of establishment is often not apparent by the range of tolerance of mature plants but can be critical to establishment of spores.



Figure 115. *Buxbaumia viridis* capsules on log. Photo by Hermann Schachner, through Creative Commons.

Sphagnum spores under wet, anaerobic conditions had much lower survivorship (dying within 2-3 years) than those under wet or periodically desiccated aerobic conditions, suggesting that respiration not only continued but was necessary for their survival (Sundberg & Rydin

2000). Refrigerated spores lasted up to 13 years. This infra-species size difference, coupled with the ability to survive freezing in upper atmosphere conditions, might permit the small spores, already better adapted for long-distance transport, to survive the greater time they are likely to be in transport.

Sphagnum provides a good example of the need for a specific nutrient. Despite the apparently good longevity of spores of *Sphagnum* species, few protonemata (Figure 73) have been observed in the field (Sundberg & Rydin 2002). Sundberg and Rydin attribute this absence to the need for phosphorus in greater concentrations than that typically found in natural waters. Various peat substrata were tested and it appeared that the amount of phosphate released was the determining factor in successful germination. Moose dung increased the success rate, as did litter from *Betula pubescens*. *Pinus sylvestris* litter did not help.

It appears that *Sphagnum* has other establishment needs as well. *Sphagnum* spp. fragments that arrived at a restoration project were unable to succeed unless they joined a *Polytrichum strictum* (Figure 116) carpet (Groeneveld *et al.* 2007). Apparently the carpet was important in keeping the developing *Sphagnum* moist. Groeneveld *et al.* considered that buffering of the temperature, making it cooler in daytime and warmer at night, may have been important as well.



Figure 116. *Polytrichum strictum* with *Sphagnum* growing between the stems. Photo by Andrew Hodgson, with permission.

Cleavitt (2002) tested the stress tolerance of fragments of pairs of rare and common species of mosses in view of their asexual dispersal potential. Habitat specificity in the three common species was more likely to correspond to physiological differences. For example, the common *Mnium spinulosum* (Figure 117) was intolerant of high light conditions and therefore only became established in the deep shade of conifer stands. The common *Bryum pseudotriquetrum* (Figure 118) was intolerant of desiccation and only became established on stream banks and other moist areas. The striking observation was that the rare *Mielichhoferia macrocarpa* (Figure 119) was tolerant of both high light and desiccation, but had the slowest rate of recovery, suggesting that some other factor contributed to its rarity, such as competition during its slow recovery, or insufficient time to recover in natural conditions before again suffering desiccation. And other factors in the environment could also be important establishment factors.



Figure 117. *Mnium spinulosum* from Europe, a species intolerant of high light conditions during establishment. Photo by Michael Lüth, with permission.



Figure 118. *Bryum pseudotriquetrum* with capsules from Europe, showing its typical wet habitat, here along a stream. Photo by Michael Lüth, with permission.



Figure 119. *Mielichhoferia macrocarpa*, a species tolerant of high light and desiccation, but one that has poor establishment success. Photo © Robin Bovey at PhytoImages website, with permission.

Bryophytes can be slow colonizers compared to some of the other taxa. Nevertheless, on Surtsey, they were among the first arrivals on the solidified lava. The typically early colonizers among the Cyanobacteria were remarkably scarce. Their most common locations were near steam vents, usually near moss clumps, particularly *Funaria hygrometrica* (Schwabe 1974; Figure 103-Figure 105). These nitrogen-fixing blue-green bacteria were especially attached to the protonemata. The moss *Racomitrium* (Figure 29), however, seemed to inhibit the growth of Cyanobacteria.

Slow Establishment

As we have noted above for *Mielichhoferia macrocarpa* (Figure 119), slow recovery may account for the lack of success in some species that arrive by diaspores. Leck and Simpson (1987) noted this problem for species recovered from a wetland diaspore bank. They identified 14 mosses, 2 liverworts, 7 ferns, and 1 horsetail, with *Bryum* sp (Figure 118) and the fern *Onoclea sensibilis* having the greatest densities. The highest densities occurred in the surface samples. Germination of spores and/or growth of these diaspores was slow compared to that required for seeds from seedbanks and they considered this slowness to be a factor in the absence of the bryophyte species on the surfaces of the wetlands.

Dispersal Limitation

A number of studies suggest that dispersal limitation is the best explanation for the patterns of abundance and distribution of bryophytes in some fragmented habitats (Pharo & Zartman 2007). But edge effects can also play an important role. Because of their small size, fast colonization-extinction rates, high substrate specificity, and dominant haploid condition, Pharo and Zartman consider them to be ideal model systems for testing the effect of fragmented landscapes on bryophyte community structure.

Nearness of source has been shown repeatedly as an important determinant of colonization, although Hylander (2009) found no relationship between colonization rate and nearness to mature forest stands for boreal forest bryophytes. This nearness component was well illustrated by Zartman and Shaw (2006) in their study of two epiphyllous species [*Radula flaccida* (Figure 120), *Cololejeunea surinamensis*] in the Amazon tropical rainforest. While extinction rates were the same for these species in both fragmented and continuous forests, colonization rate was much greater in the continuous forest sites (Figure 121).

Kimmerer (2005) demonstrated the importance of dispersal at a small scale in the colonization of treefall mounds in the Adirondack Mountains, USA. When spores and fragments of *Polytrichum ohioense* (Figure 122), *Dicranella heteromalla* (Figure 123), *Atrichum angustatum* (Figure 5), *Diphyscium foliosum* (Figure 124), and *Pogonatum pensilvanicum* (Figure 125) were sown on the mounds, these species became established, with the highest success occurring with fragments. Under natural conditions, only 1-2 of a possible 13 species established on any single mound and likewise, in the experiment, sown propagules were far more successful than natural dispersal to mounds with no added propagules.

Kimmerer considered this to be strong evidence of dispersal limitation on treefall mounds.



Figure 120. *Radula flaccida* with gemmae, an epiphyllous species that does best in continuous forest. Michaela Sonnleitner, with permission.

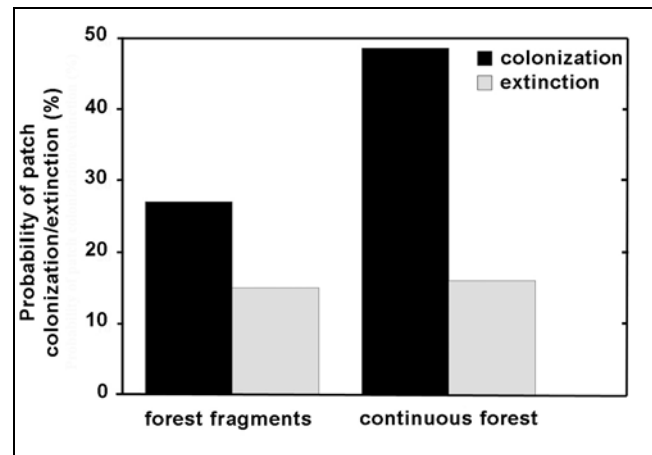


Figure 121. The colonization and extinction rates of *Radula flaccida* and *Cololejeunea surinamensis* on epiphylls in the Amazon tropical rainforest. Data for the two liverworts were very similar and thus were combined. Redrawn from Zartman & Shaw 2006.



Figure 122. *Polytrichum ohioense*, a species that seems to be dispersal limited when colonizing treefall mounds. Photo by Janice Glime.



Figure 123. *Dicranella heteromalla* on a soil bank. Despite its numerous capsules, its fragments are more successful at establishment on treefall mounds. Photo courtesy of Eric Schneider.



Figure 124. *Diphyscium foliosum* male plants (green) and female capsules and perichaetial leaves. Fragments are more successful in establishment than are spores. Photo by David Holyoak, with permission.



Figure 125. *Pogonatum pensilvanicum* with capsules on a soil bank. Note the ground cover of protonemata and absence of leafy gametophytes. Photo by Bob Klips, with permission.

Recolonization

In some habitats, bryophytes are among the first organisms to colonize a disturbed site. These are generally fugitives and other species that cannot tolerate the competition of tracheophytes. They take advantage of the sun but must tolerate greater drying than the species living in forested habitats. But they must also have good dispersal capabilities to arrive there and thrive before the competition arrives.

Arrival in disturbed habitats can be extensive, as Greven (1994) observed in an experimental garden. Between 1972 and 1991, 91 species arrived in the garden. The greatest number of taxa occurred on the chalk soils (40 spp), with peat having the fewest (6 spp). Even several rare taxa arrived.

In an urban environment, a community can re-establish itself in 1-2 years (Nehira & Nakagoshi 1987). Thalloid liverworts and pleurocarpous mosses were the first to regenerate, ahead of the acrocarpous mosses. This is somewhat unusual as the acrocarpous mosses typically have more asexual diaspores than do pleurocarpous mosses, but regeneration may have occurred from remnants and fragments, a dispersal mechanism common among pleurocarpous taxa. Regrowth occurred primarily in the spring and autumn, despite little seasonal variation in the number of airborne diaspores, suggesting the importance of rainfall and perhaps cool temperatures.

Forests

The slow rate of recolonization in harvested regrowth forests is illustrated by the smaller number of species present, presumably due to the slow rate of dispersal and establishment of species common in old-growth forests (Cooper-Ellis 1998). In the Central Cordillera of Colombia, Corrales *et al.* (2010) considered the dispersal of propagules among the various forest types to be the primary mechanism driving the regional pattern of bryophyte distribution.

Proximity to other suitable bryophytes seems to be a major factor in what species will become established after a disturbance. Even in the limited microcosm of a leaf, Cobb *et al.* (2001) found that bryophytes colonizing *Acer macrophyllum* leaves (epiphyllous) in Olympia, Washington, USA, after experimental removal of the epiphylls, were primarily due to lateral encroachment (75%). Only ~8% of the exposed area had been recolonized one year after removal of bryophytes, reaching 27% after three years. The 25% not colonized by encroachment included incompletely removed plant parts and aerially dispersed diaspores.

On the other hand, in young boreal forest stands, there was no indication of higher colonization by bryophytes close to the mature stands where bryophytes were undisturbed (Hylander 2009). Following a forest fire, bryophytes that recolonize can either arrive anew or survive the fire. Survival of the fire could be the result of migrating to a safe site during the fire (*i.e.*, local dispersal to safety) or by enduring the conditions (Hylander & Johnson 2010). Endurance can be due to wetness, burial, or positioning in the protection of logs, rocks, or other blockades to the fire. Hylander and Johnson (2010) found an average of three refugia per 50 x 50 m reference plot,

with a mean of 4.8 bryophytes associated with them. But in the area that had been burned, only a mean of 1.5 species could be found in the refugia. However, other factors seemed to be more important than refugia. There was no correlation between the number of refugia and the number of forest species that colonized the plots. The refugia were mostly on rocky or mesic sites, not wet sites. The importance of these refugia most likely depends on the intensity and nature of the fire. A ground fire will have a very different effect from a crown fire.

Schmalholz and Hylander (2010) examined a similar question regarding the role of forest floor refugia in response from clear-cut logging. They found survival differences based on microtopography. The shelter of boulders and stumps resulted in significantly more survival (~30%) than on level forest floor (10%) for transplanted bryophytes. These boulders and stumps also resulted in less change in species composition.

Evidence from Europe suggests that the same forest can be colonized by a bryophyte species multiple times. Cronberg *et al.* (2002) found repeated recruitment among populations of *Hylocomium splendens* (Figure 57) on 10 Baltic islands. He identified 103 haplotypes among 694 shoots with number of clones increasing significantly with increasing age of the islands. He likewise showed that the number of genotypes of *Plagiomnium affine* (Figure 126) correlated with the age of the forest stand in Europe (Cronberg 2005). Using 23 allozyme loci and six populations of *P. affine*, they sampled 602 shoots and found 16 haplotypes. Among these, 12 were unique to single populations. Allelic richness and diversity were significantly correlated with forest age at the ramet level but not quite so at the genet level.



Figure 126. *Plagiomnium affine*, a species for which the number of genotypes correlates with forest age. Photo by Michael Becker, through Creative Commons.

Patch Fragmentation

Logging has an impact on the distribution of bryophytes. Isolated patches that remain may be invaded by new species and disturbed areas will both lose old species and gain new ones. In the temperate rainforest of British Columbia, Canada, Baldwin and Bradfield (2007) compared bryophytes on the forest floor, downed logs, and tree bases. They found that the dispersal-limited groups

such as perennial stayers and the microclimate-sensitive groups declined in species richness or frequency as patch size decreased. These microclimate-sensitive groups included those from closed canopy, log-dwelling species, and liverworts. Colonists and open canopy species showed little relationship to patch size. In the patch size range of 0.6-63.6 ha, most of the patch size effects disappeared when the three smallest patches (0.6-1.8 ha) were not included in the analysis. Therefore, patch sizes of at least 3.5 ha seem to provide suitable habitat to sustain the diversity of bryophyte functional groups in this temperate rainforest habitat. It is likely that part of this decrease in diversity is due to dispersal limitation.

Summary

Most bryophytes are adapted for wind dispersal, with the occasional updraft or gust permitting somewhat greater distances. Epiphytes gain height through their host. However, the majority of spores seem to land within 2 m of their parents. It follows that spore density in the atmosphere decreases with distance from the source and increases with height of the colony.

Members of the **Polytrichaceae** have a membrane connecting their teeth and disperse spores by disturbance such as rain drops. These are ejected horizontally and apparently do not travel far.

Bryophytes that live on temporary and disturbed substrata, such as logs and arable land, require either good dispersal or the ability to survive in diaspore banks.

Tracheophyte dispersal models have limited applications to bryophyte dispersal. Bryophyte spores are much smaller than seeds and lack multiple layers of tissues to protect them. Vegetative diaspores may mimic some of the elongate shapes, but spores tend to travel farther than vegetative propagules.

Bryophytes seem to support the concept that "everything is everywhere, but the environment selects." Unfavorable light, photoperiod, substrate, temperature, and moisture conditions can prevent establishment of a species once it arrives. This concept is supported by the small size of spores, the distribution patterns, and patterns of establishment on newly formed islands.

Molecular Clocks can be used to estimate time of arrival and help us to trace the dispersal routes.

Weather, dust storms, and fires can play a significant role in creating air currents, protecting from UV, and maintaining moisture.

Even diffusion models can help us understand dispersal, but size, falling velocity, and access to the air stream all have roles in the distance travelled. Long-range dispersal is facilitated by wind, requiring updrafts to get spores into the atmosphere. There the spores must survive UV light, desiccation, and extremes of temperature, especially sub-freezing temperatures. In some areas there is clear evidence of **stepping stone** progression once the first propagule arrives and succeeds in the area.

Small spores travel the farthest; large spores provide more energy for the start of growth. Spores

range from 5 μm in *Dawsonia* to 310 μm in *Archidium*, with numbers per capsule ranging from 4 in *Archidium* to 50 million in *Dawsonia*. Most bryophyte spores range about 20-100 μm and hence weigh about 0.004 μg to about 0.52 μg , all falling in the size category where wind dispersal is expected. Few animal dispersers are known for bryophytes. Most spores seem to fall within 2 m of their parents, but only a few need be caught into updrafts in order to accomplish long-distance dispersal. Limited **gene flow** between populations, demonstrated by genetic variation between them, suggests that most populations arise from a single propagule and that there is little mixing. This is further supported by the lack of genetic variation within populations.

Height of origin, such as epiphytes or species on walls and boulders increase dispersal effectiveness. Many dispersal periods are correlated with dry weather, especially for small spores, but at least in some locations, spores can be trapped from the atmosphere year-round. Some capsules require more than a year to develop whereas others mature in a few weeks. Few data exist that identify the species of atmospheric travellers, but certainly *Funaria hygrometrica* is one of them. Often the spores that are travelling are different from the species of a particular environment.

Long-distance dispersal is limited by drought tolerance and UV radiation (lethal for most species). For Neotropical liverworts, there is no dispersal advantage based on spore size, bisexuality among small-spored species, presence of chlorophyll, verrucosity of spore wall, and presence of gemmae. Bisexuality seems to have a positive advantage in large-spored (>35 μm) species. Species with greater source distributions and greater area of suitable destination habitats have greater dispersal potential. Dark-colored spore walls may protect against UV radiation. **Callose** deposits on the spore, waxy **sporopollenin** on the surface, and in most mosses a **perine** layer, all may contribute to protection of the spore.

Wet freezing has equal effect on transoceanic and endemic species. Both spores and sporelings survive longer with good drought tolerance. Among large-spored species (>25 μm), xerophytes survive dispersal better than mesophytes or hygrophytes. Dispersal by water is possible in many taxa, with survival times ranging from a few days to many months.

Once arriving, spores and vegetative diaspores must adhere. For spores, verrucose surfaces can facilitate catching on something, such as tree bark.

Because of the limits of dispersal, ability to remain viable in soil banks, and changes in environmental conditions, the bryophytes that become established following a disturbance may differ considerably from the original flora.

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CHAPTER 4-9

ADAPTIVE STRATEGIES: SPORE DISPERSAL VECTORS

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CHAPTER 4-9

ADAPTIVE STRATEGIES: SPORE DISPERSAL VECTORS



Figure 1. Capsules of *Splachnum ampullaceum*, adapted for fly dispersal by both red colors and their odor. Note the special landing platform (**hypophysis**) below the cylindrical capsule. Photo by Michael Lüth, with permission.

Dispersal Types

Gao *et al.* (2000) examined the Chinese bryophyte flora and concluded that there are five classes of spore dispersal. These are wind dispersal, vapor-wind dispersal, water dispersal, decay dispersal, and insect dispersal. But more digging reveals that additional dispersal agents may be at work among the animals, including earthworms, spiders, molluscs, birds, and even mammals.

Hughes *et al.* (1994) concluded that the availability of specific dispersal vectors seems to have no influence on dispersal mode. I think that one could use flies that visit the **Splachnaceae** on dung to argue against that conclusion, but there do not appear to be any studies that attempt to correlate dispersal mode with availability of the vector.

For spores to gain access into the atmosphere, they must be expelled away from the capsule and join wind currents before they fall to the ground. One can flick a newly opened capsule and see clouds of spores emitted. It is likely that deer, rabbits, squirrels, and various small rodents bump these extended capsules, likewise sending up clouds of spores. To this end, the **peristome teeth** (Figure 2-Figure 4) of many mosses work like a saltshaker and permit only a portion of the spores to escape in one event. This helps to insure that dispersal takes place over an extended period of time and may then encounter more climatic conditions wherein some are suitable for good or even long-distance dispersal.



Figure 2. Peristome teeth of *Funaria hygrometrica*, showing the chambering that helps in the slow dispersal of spores. Photo by Michael Lüth, with permission.

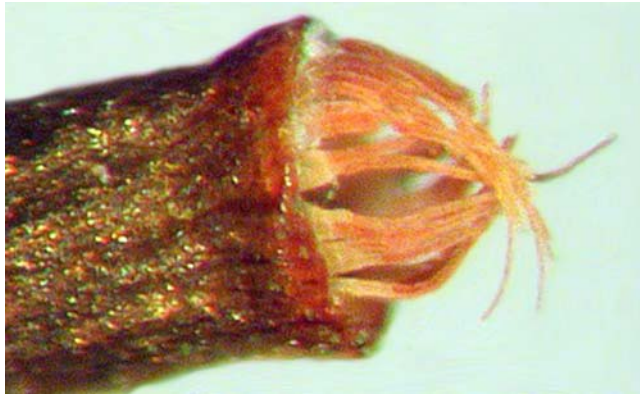


Figure 3. Peristome teeth of *Aloina aloides* showing spaces between teeth that create a saltshaker effect to slow dispersal. Photo by Michael Lüth, with permission.

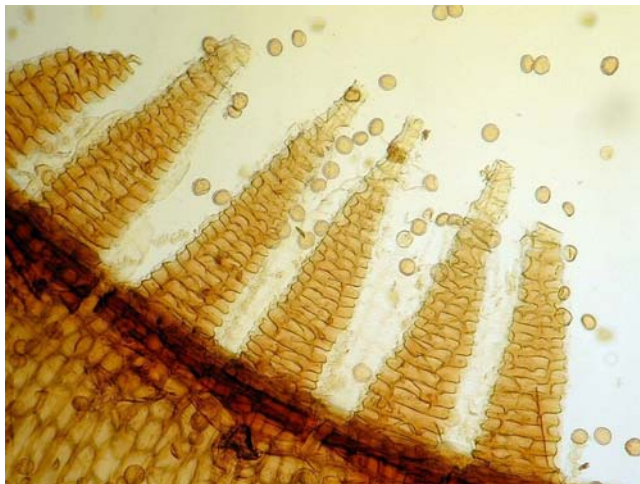


Figure 4. Peristome teeth and spores of *Ptychostomum pendulum*. Photos by Michael Lüth, with permission.

Wind Dispersal

Wind dispersal is assumed to be the rule among most bryophytes. But few data were available to support that concept for long-distance dispersal.

As we discussed in examining long distance dispersal, any propagule released from a greater height or elevation has a greater probability of being exposed to greater wind velocities (Greene & Johnson 1996). This means that greater heights increase the opportunities for wind dispersal. Campbell *et al.* (2001) contend that mosses have high immigration potential due to the wind-dispersal ability

of their spores. This would seem to argue against the conclusions of Hughes *et al.* (1994) that the availability of specific dispersal vectors has no influence on dispersal mode. As already discussed in the previous sub-chapter, successful wind dispersal relates to release height and falling time (slow for spores due to small size). Wing loadings in bryophytes are very low and probably have insignificant effect. Release height can be increased by explosive behavior of some capsules, and location on trees or at higher elevations likewise increases the opportunities to become airborne..

Lönnell (2011) reminds us that according to Stoke's law (Figure 5) spores can travel farther than larger diaspores of the same shape and density, given the same wind speed. [Stoke's Law: If particles are falling in a viscous fluid by their own weight due to gravity, then terminal velocity, also known as settling velocity, is reached when this frictional force combined with the buoyant force exactly balance the gravitational force.] Lönnell compared small seeds to large seeds, stating that, even if larger seeds can increase the buoyancy with features like pappi or wings, small seeds can still travel farther. Bryophyte spores lack such features as wings, but do possess pappi and other surface features. I am unaware of any study that has examined the role of variations in these markings as a means to facilitate wind dispersal. Perhaps they do, however, create buoyancy in water, permitting them to float and thus get dispersed farther.

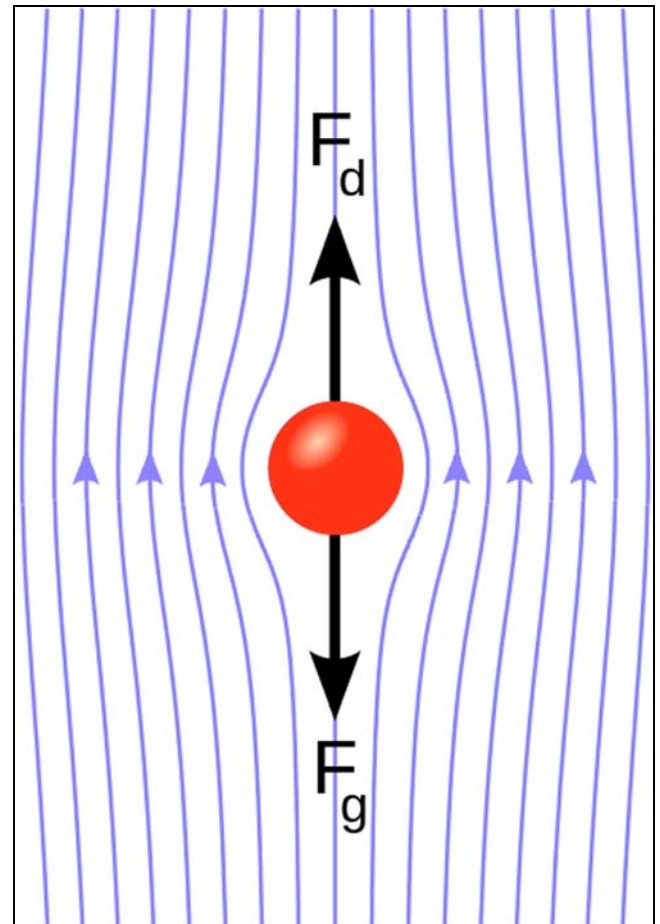


Figure 5. Stokes sphere showing movement of fluid around it. F_d is the frictional force, known as Stokes' drag. F_g is the force by gravity. Image from Wikimedia Commons.

We lack measures of density of bryophyte spores in the atmosphere, but experience with other organisms and particles are instructive. Schlichting (1978) tells us that there are 0.3-7.5 billion particles greater than 0.2 μm in diameter in one cubic meter of "clean air." And joining these organisms are spores of bryophytes. Puschkarew (1913) found an average of 2.5 protozoan cysts in a cubic meter of air, attesting to the success of somewhat larger structures being transported.

In sampling airborne algae in Michigan, USA, Schlichting (1964) found the greatest numbers of algae and protozoa between noon and midnight on cloudy days, with more during July and August than during September through May, although this may have related more to innate life cycles than to that year's weather conditions. The wind elevation angle (*i.e.*, horizontal vs vertical) seemed important in determining the number of organisms present; wind direction and speed seemed less important. Updrafts were more important than downdrafts or horizontal wind. Rainfall during the preceding 24 hours was detrimental to organism presence, most likely quickly washing them from the atmosphere. Sizes of the most common propagules ranged from the one-celled alga *Chlorella* with diameters of ca. 2-8 μm to those of cysts of the protozoan *Oikomonas*, for which living cells range up to 100 μm or more (without knowing the species, we cannot determine the size of the cysts, but they are likely to be similar). This range encompasses the majority of spore sizes of bryophytes.

But wind is constantly changing, and averages can be misleading. Sudden changes in direction can stir up tiny tornadoes that may dislodge and uplift spores. This might be especially true on glaciers. Bonde (1969) collected plant propagules from wind-blown debris on St. Mary's Glacier at 3350 m. He found 35 species of seed plants, but he also found viable parts of the moss *Polytrichum piliferum* (Figure 6), lichens, and *Selaginella*.



Figure 6. *Polytrichum piliferum*, a moss whose fragments are known from wind-blown debris. Photo by David T. Holyoak, with permission.

In the Southern Hemisphere, it appears that wind has played an important role in geographic distribution of bryophytes. Muñoz *et al.* (2004) found that there was a stronger correlation of floristic patterns with wind patterns than with geographic proximities, supporting wind dispersal for the arrival of many organisms in the Southern Hemisphere. These wind patterns followed "wind highways" that resulted in directional dispersal and distribution.

Felícísimo *et al.* (2008) attempted to understand the role of global wind patterns in dispersal by not only wind data but also the pathway of a tracked seabird, the Cory's Shearwater (*Calonectris diomedea*). Birds are able to locate the pathways that require the least energy to carry them to their destination, going higher or lower, following mountains or other areas where updrafts and wind movement help to carry them where they need to go. The shearwaters followed the pathways predicted by the air pattern model, but when they reached the Atlantic sector of the Intertropical Convergence Zone, they were hindered by the near-surface westerlies. Only after these westerlies ceased were the birds able to cross this zone. Hence, we have evidence for seasonal differences in the most energy-effective pathways.

To understand the diaspore rain, it is necessary to trap the propagules, then culture them. Ross-Davis and Frego (2004) report success with diaspore traps using nutrient agar plates. These trapped diaspores grow well from both spores and vegetative propagules at indoor ambient conditions – so well that they need to be transplanted due to crowding. But patience is required; it takes nine months for them to reach a recognizable stage.

Splachnaceae

This family is best known for its spore dispersal by flies. But Walsh (1951; see also Bryhn 1897) has observed an alternative method – wind dispersal. He observed that in *Splachnum sphaericum*, when the capsule dried, the **peristome** teeth became reflexed, adhering to the outside of the capsule. From the inside, the spores were pushed out as the capsule dried and shrank. And the **columella** extruded from the capsule – a phenomenon known in only a few mosses. The spores form a ring around the top of the capsule and adhere to each other in clusters. The teeth remain hygroscopic and withdraw when moisture returns. Furthermore, the spores likewise withdraw and the capsule once more becomes turgid and swollen. This extension and intrusion of peristome and spores can continue to occur as moisture changes occur. When the peristome reflexes, it typically carries adhering spores away from the capsule.



Figure 7. Young capsules of *Splachnum rubrum* with **operculum** (cap) still intact on all but one capsule. Note that the umbrella-shaped structure is a **hypothesis** that occurs at the base of the capsule. Spores are housed inside the cylindrical structure above it. Photo by Michael Lüth, with permission.



Figure 8. Capsules of *Splachnum rubrum* that have shed their opercula. Note the exerted teeth and the ring of spores at the capsule opening. Photo by Michael Lüth, with permission.



Figure 9. Peristome of *Splachnum ampullaceum* with teeth reflexed against capsule and columella extruded at the center of the spore mass. Photo by Janice Glime.

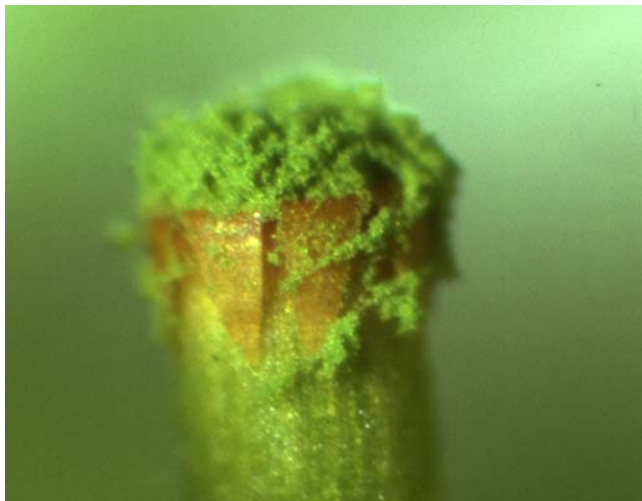


Figure 10. Peristome of *Splachnum ampullaceum* showing peristome teeth reflexed against the capsule and spore clusters clinging to them. Photo by Janice Glime.

When struck by a strong wind, the extruded clusters may extend from the capsules in either clumps or threads. Sometimes the wind causes the threads to bend back upon themselves, in which case the thread more closely resembles a clump. But in some cases the clusters or

threads may break loose, effecting dispersal. The stickiness of the spores is important in assuring that both genders arrive on the new substrate, hence making spore production possible in that generation. But Walsh was unable to observe the fate of these escaped spores. The dung substrate necessary for the life cycle to continue is rare relative to all the other possible landing substrates available. I would think that even though wind dispersal is possible, it would be rare that successful landing on a suitable dung substrate would occur.

Liverworts

Schuster (1966) considered liverwort dehiscence and spore dispersal to be timed to occur when there would normally be strong, drying winds to dry the outer layer of the capsule wall, causing the valves to curl backward. Since outer walls would dry first, they would be more contracted than inner walls.

Liverworts are aided in spore dispersal by elongate structures with spiral thickenings called **elaters** (Figure 11). These respond to changes in moisture, causing walls of cells between spirals to contract, thus resulting in twisting of elaters and contortion or bending of cells. When the elater reaches a certain point of tension due to remaining water adhering to walls of drying cells, it suddenly releases the remaining water and jerks into its original shape, thrusting nearby spores into the air. There are variations on this theme, discussed in the subchapter on Marchantiophyta. Schuster (1966) considers that in liverworts, numerous small spores (6-18 μm in diameter) are an adaptation for wind dispersal.

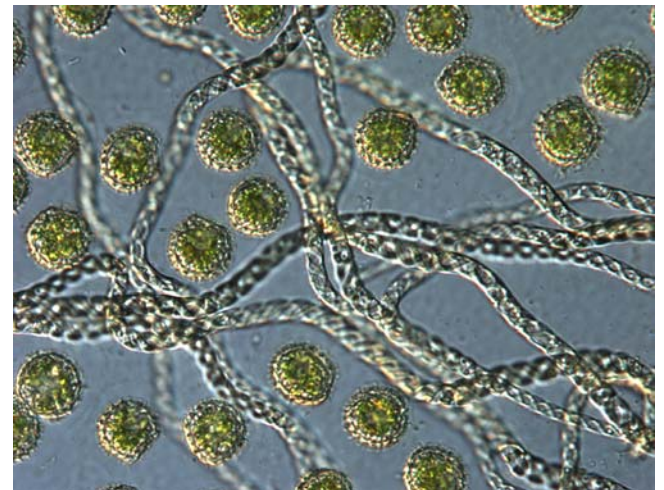


Figure 11. *Hymenophyton* sp. spores and elaters. Photo by Karen Renzaglia, with permission.

Invasive Species

The invasive *Campylopus introflexus* (Figure 12) has spread rapidly over Europe, apparently by its small spores (Hassel & Söderström (2005). Once there, it spreads rapidly by programmed fragmentation of deciduous leaves. *Orthodontium lineare* (Figure 13), another invasive species in Europe, spreads by numerous small spores. It lacks vegetative reproduction, although its ability to grow from fragments remains to be tested. Because it must establish and spread by spores, it requires about thirty years

before it is able to produce mature spores; *Campylopus introflexus* requires only ten. It appears that the spread of spores in both species is predominantly (or entirely) by wind.



Figure 12. *Campylopus introflexus*, an invasive weed in Europe. Photo by Michael Lüth, with permission.



Figure 13. *Orthodontium lineare*, an invasive species in Europe. Photo by Michael Lüth, with permission.

Decay Dispersal

Some capsules lack peristome teeth and do not dehisce (cleistocarpous capsules; Figure 14-Figure 17). In these cases, the capsule must decay or be eaten for spores to escape.



Figure 14. *Goniomitrium enerve* with cleistocarpous capsules. Photo by David Tng, with permission.



Figure 15. *Physcomitrella patens* cleistocarpous capsule. Note neck of archegonium forming a dark projection at the tip of the calyptra. Photo through Wikimedia Commons.

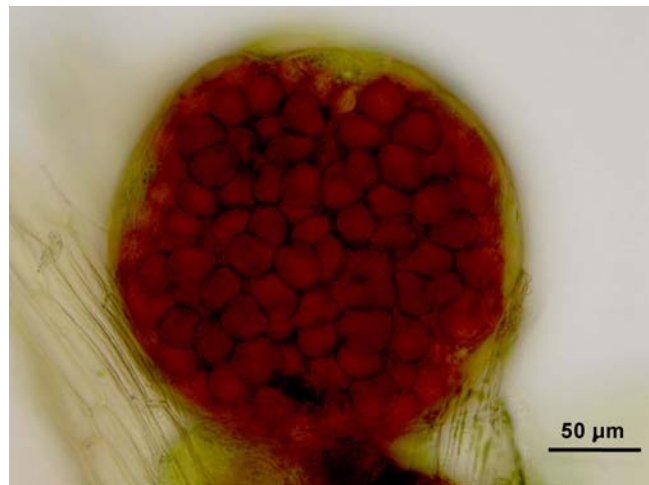


Figure 16. *Micromitrium synoicum* cleistogamous capsule. Photo from Duke University Herbarium, through Creative Commons.

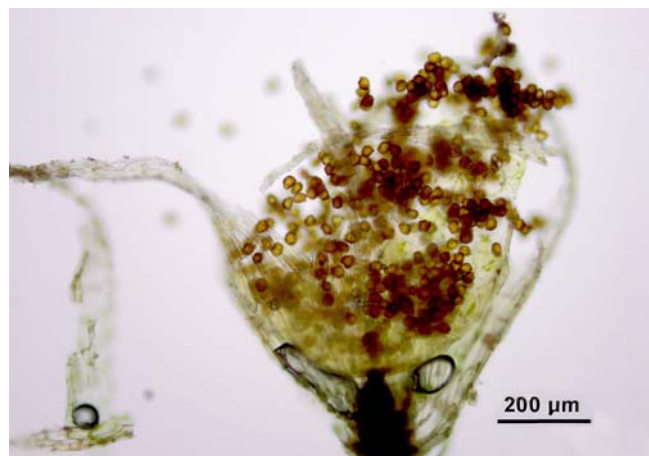


Figure 17. *Micromitrium synoicum* cleistogamous capsule breaking apart, showing spores. Photo from Duke University Herbarium, through Creative Commons.

Even some capsules with an operculum and peristome may use decay as a means of releasing spores. In *Fontinalis novae-angliae* (Figure 18) and *F. dalecarlica* (Figure 19), abrasion by flowing water and debris (in New

Hampshire, USA) often erodes the capsule wall away with the operculum still intact. The capsules in this genus tend to be quite thick, perhaps an adaptation against premature erosion. But the question remains, are the spores still viable in these older capsules that seem to be heavily endowed with phenolics, or are these capsules that aborted before reaching the maturity needed for normal dehiscence and dispersal? Since these spores disperse in late winter, observations on the actual dispersal seem to be lacking, my own included.

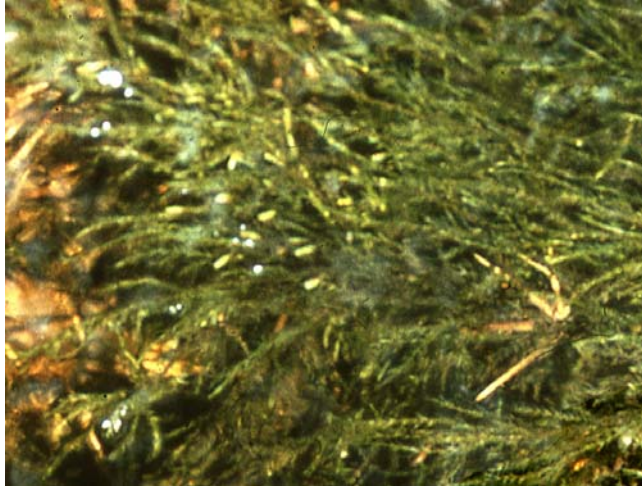


Figure 18. *Fontinalis novae-angliae* with capsules. Photo by Janice Glime.



Figure 19. *Fontinalis dalecarlica* with capsules. Photo by Janice Glime.

I have observed capsules in these two species, still submersed, but not yet mature. Korsteli (2003) observed very different behavior in *Fontinalis antipyretica* (Figure 20) from the dense capsule walls I observed after spring runoff. He reported that sporophytes in this species are produced under water, but that dry conditions were needed for the capsule to dehisce. Under such conditions, the operculum tears loose, lifted by hygroscopic movements of the exostome teeth. Spores are released by reversible changes in the shape of the capsule! Misha Ignatov (Bryonet 29 March 2013) observed the teeth in the lab and watched them gyrate as they dried (Figure 21).



Figure 20. *Fontinalis antipyretica*. Photo courtesy of Betsy St. Pierre.

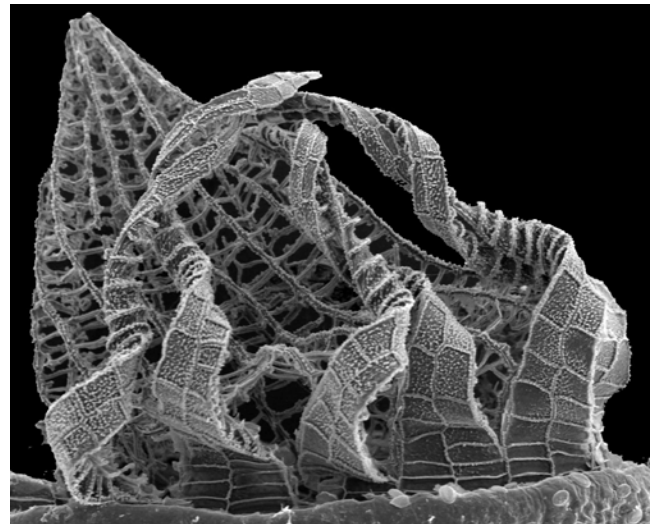


Figure 21. *Fontinalis* sp. peristome (SEM) showing the contorted teeth as they dry. Photo by Misha Ignatov, with permission.

Buxbaumia aphylla (Figure 22) seems to disperse its spores more commonly by having the capsule split across the broad, flat upper surface. The capsule wall peels back, exposing the spores (Figure 22). In my observations, this appears to be the typical case – I have not found capsules with intact walls and exposed teeth, the condition one would expect for dispersal through the capsule opening. In fact, my early observations led me to think these capsules were being eaten, but careful periodic observations by my graduate student, Chiang-Liang Liao, proved me wrong. Nevertheless, once the spores are exposed, it appears some insects may indeed feed on them and potentially disperse them. Müller (2012) found that adult fungus gnats (Mycetophilidae; Figure 23) in Germany feed on these spores (Figure 23-Figure 24) and thus might carry spores on their bodies, consequently dispersing them.



Figure 22. *Buxbaumia aphylla* showing the peeled back capsule wall that exposes the spores. The lower capsule has lost its operculum and the teeth are showing. Photo by Janice Glime.



Figure 23. *Buxbaumia aphylla* with fungus gnats eating spores from the few remaining capsules. Photo by Jörg Müller, with permission.



Figure 24. *Buxbaumia aphylla* capsules partially eaten by fungus gnats. Photo by Jörg Müller, with permission.

It may surprise the novice to find that in the fly-dispersed family Splachnaceae exist non-fly-dispersed species that require capsule decay for release of spores from the capsules. In these species, there are no teeth and the capsule does not dehisce. Among these are *Voitia nivalis* (see Figure 25) (Goffinet & Shaw 2002) and *Tayloria callophylla* on soil (Figure 26); others are epiphytic except for two additional coprophilous but cleistocarpous (capsule not opening) species.



Figure 25. *Voitia hyperborea* in Svalbard, showing cleistocarpous capsules. Photo by Michael Lüth, with permission.



Figure 26. *Tayloria callophylla* with capsules, from New Zealand. This is a species that occurs on soil and lacks the expanded hypophysis typical of *Splachnum*. Photo by Zen Iwatsuki, with permission.

Carrión *et al.* (1995) cite xerophytic *Phascum* spp. (Figure 27), *Pterygoneurum* spp. (Figure 28), and *Acaulon* (Figure 29) as sharing cleistocarpous capsules, large spore size, and highly sculptured spores. But interesting anomalies exist. *Pterygoneurum sampaianum* (Figure 30) has two spore sizes and spore wall thicknesses. Carrión *et al.* suggest this permits most germinations to occur in suitable habitats of parents while allowing for at least some longer transport to new locations. Vitt (1981) surmised that cleistocarpy was important in ephemeral habitats, where large spores have a better chance of surviving until the conditions become favorable again. Having two types of spores would be advantageous in these conditions.



Figure 27. *Tortula acaulon* (= *Phascum cuspidatum*) with cleistocarpous capsules. Photo by Jan-Peter Frahm, with permission.



Figure 28. *Pterygoneurum ovatum* with ovate capsules. Photo by Kristian Peters, with permission.



Figure 29. *Acaulon triquetrum* with cleistocarpous capsules. Photo by Michael Lüth, with permission.



Figure 30. *Pterygoneurum sampaiianum* in sand, a species with two spore sizes. Photo by Jan-Peter Frahm, with permission.

Surely through such a long period of evolution some of these cleistocarpous capsules must have evolved invertebrate partners that help in the destruction of the capsule wall. Or is it bacteria, or fungi, that do the deed? But certainly some open as a result of torque resulting from drying.

Animal Dispersal

Volk (1984) considered animals to be the most important means of dispersal for the **Marchantiales** in Namibia, suggesting that dispersal was facilitated by the spore ornamentation.

When we think of animal dispersal, we think of "velcro" plants that attach their propagules by small hooks to the fur of their host, or we think of seeds passing through

the digestive tract unharmed while the host benefits from the surrounding fruit. But are bryophytes too small to utilize such large animal carriers? Are capsules good substitutes for fruits? We must think on a small scale, and the obvious disperser seems to be insects, those creatures upon which the pollen grain must so often depend. But most people know only about the ability of the **Splachnaceae** to hitch a ride on an unsuspecting insect, the fly, to achieve the dispersal of their spores. It appears we have been missing something.

Earthworms

As earthworms pass soil particles through the gut, they also transport bryophyte diaspores. Van Tooren and During (1988) found that spores were more successful at germination than vegetative diaspores when taken from earthworm castings (Figure 31). Interestingly, During (1986) found that spores from more than 1 cm down were more likely to germinate than those in the first centimeter. He suggested a higher mortality rate among those in the first centimeter, or that most of the spores were washed down to deeper layers. It is likely that a spore in that first cm would get enough water and light to effect germination, but that they might not remain wet enough, or have enough light, to survive after germination; they might also get water frequently, activating respiration, but having insufficient light to germinate, thus losing considerable energy each time they get wet. Nevertheless, it is also a good hypothesis that many got washed down to lower layers.



Figure 31. Earthworm castings, a potential means of bringing bryophyte diaspores to the surface. Photo by Muhammad Mahdi, through Creative Commons.

Gange (1993), examining primarily fungal spores, found that earthworm castings had higher concentrations of spores than did the surrounding soil. If they likewise concentrate bryophyte spores, this could be an effective dispersal mechanism, perhaps placing diaspores into the diaspore bank, or removing the diaspores from the diaspore bank, despite the high mortality rate seen by Van Tooren and During (1988). A high mortality is not 100%, so those spores that do survive might be effective in later establishment.

Insects and Spiders

It is likely that arthropods such as insects and spiders have a greater role in bryophyte spore dispersal than we

had imagined. Such characteristics as hairs on the arthropod or sticky spores facilitate such dispersal.

Ignatov and Ignatova (2001) report that small spiders, mites, and beetles that walk among the cave moss (*Schistostega pennata*) (Figure 86) plants become "more or less dirty" with spores. Smooth-bodied insects seem to be poor carriers, but hairy arthropods such as spiders, especially *Trochosa* spp. (Figure 32), and harvestmen (*Opiliones*) are more likely to carry the sticky spores.



Figure 32. *Trochosa spinipalpis*, a hairy spider that might contribute to dispersal of sticky spores. Photo by Jørgen Lissner, with permission.

Schuster (1966) reports observing lathridiid beetles feeding on spores of the leafy liverwort *Lophozia porphyroleuca*, but alas, that was in a herbarium. In fact, one of the bits of "evidence" often cited to say that bryophytes are inedible is the lack of dermestid beetles found in bryophyte herbaria, whereas seed plants must be stored with mothballs if we don't want them to disappear into the guts of these beetles. But this one observation of a lathridiid beetle eating liverwort spores does not prove that they ever disperse them in nature, or for that matter, even eat them in nature. On the other hand, this family of beetles is known to eat fungal spores, digest the exine, and disperse them in viable condition from the other end of the gut. So maybe...

Ants

A somewhat more believable story, but one Schuster (1966) considers least credible, is that Szepesfalvy considers ants to disperse spores of the liverwort *Athalamia hyalina* (Figure 33) because ants use spores (Figure 34) as food (Loria & Herrnstadt 1980) and these spores are often found injured. Based on this evidence, it is likely that some are also dispersed unharmed.



Figure 33. *Athalamia hyalina*, a liverwort that serves as food for ants. Photo by Adolf Ceska, with permission.

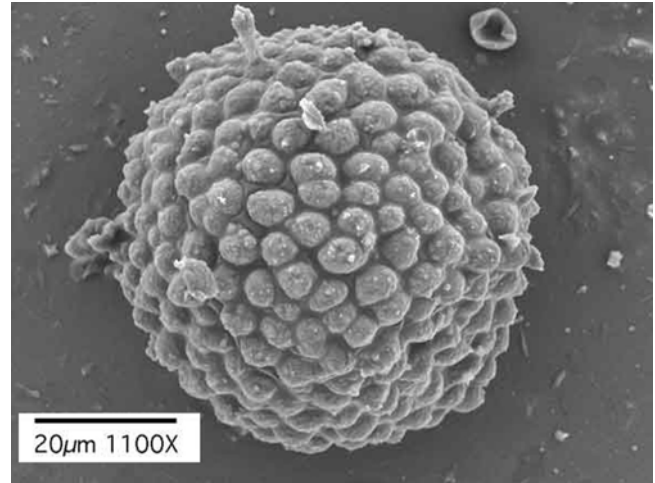


Figure 34. *Athalamia hyalina* distal spore wall SEM. Photo by William T. Doyle, with permission.

Rudolphi (2009) considered that the ant *Lasius platythorax* might be a passive dispersal agent of the asexual propagules of the moss *Aulacomnium androgynum*. Both the moss and the ants occur on dead wood in Swedish forests. Experiments showed that 33% of the ants has gemmae adhering to them within less than two minutes of exposure to the mosses. Half of these gemmae continued to adhere to the ants for approximately 4 hours, indicating that the ants could be effective dispersal agents.



Figure 35. *Lasius platythorax*, dispersal vector for gemmae of *Aulacomnium androgynum*. Photo by April Nobile, <www.antweb.org>, through Creative Commons.



Figure 36. *Aulacomnium androgynum* showing clusters of gemmae. Photo by Des Callaghan, with permission.

Aquatic Insects

Even aquatic insects may contribute to dispersal. Revill *et al.* (1967) cultured the flora and fauna occupying the surfaces of four aquatic Diptera [*Tipula triplex* (see Figure 37), *Bittacomorpha clavipes* (Figure 38), *Chaoborus punctipennis* (see Figure 39), *Chironomus* sp. (as *Tendipes*; Figure 40)]. Using 51 cultures from washings, they found algae, protozoa, Cyanobacteria, and moss protonemata. *Bittacomorpha clavipes* carried significantly more of these organisms than the other three species.



Figure 37. *Tipula abdominalis* larva. Photo through Creative Commons.



Figure 38. *Bittacomorpha clavipes* adult. Photo from William Vann at Edupics, free for educational use.



Figure 39. *Chaoborus flavicans* larva at water surface. Photo by Malcolm Storey (DiscoverLife), through Creative Commons.



Figure 40. *Chironomus* larva. Photo by Gerard Visser <www.microcosmos.nl>, with permission.

Sticky Spores

Ignatov and Ignatova (2001) found that spores of *Schistostega pennata* (Figure 41-Figure 42) were covered with a sticky substance, much like spores in the *Splachnaceae* (Figure 43-Figure 46). This substance causes many spores to stick together and prevents effective transport by wind. On the contrary, the spores are better adapted to transport by arthropods and other animals to which they adhere. Although Gaisberg and Finckh (1925) reported their inability to be transported by wind, commenting that they are glued together and are dispersed through animals, it appears that most bryologists have paid little attention to the sticky nature of the spores or their mode of transport until the publication of Ignatov and Ignatova in 2001.

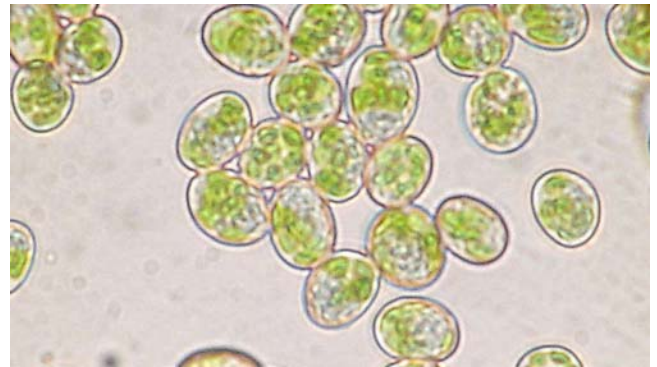


Figure 41. Elliptical spores of *Schistostega pennata* demonstrating tendency to stick together. Photo by Misha Ignatov, with permission.

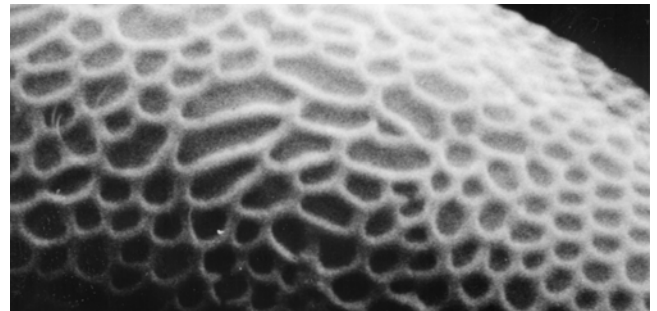


Figure 42. SEM image of spore surface of *Schistostega pennata* showing sticky perine. Photo by Misha Ignatov, with permission.

The *Schistostega pennata* sporophyte (Figure 86) shares another unique character with *Splachnaceae* (cf. Koponen 1990); its seta continues growth after the capsule has opened. But it also shares with liverworts the habit of producing its capsule before the seta elongates. In fact, it may even lose its operculum before elongation begins. The seta itself is unique, having long-rectangular, thin-walled

cells with round chloroplasts scattered in such a way that the seta appears to have be fluorescent.

Using sticky tape to trap insects near *Schistostega pennata*, Ignatov and Ignatova (2001) found spores, probably of *S. pennata*, adhering to adult members of the fly family **Dolichopodidae**. They also found that some ants (*Formica rufa*) and beetles (*Geotrupes stercorarius*; Figure 90) climbed among the *S. pennata* and that the beetles carried spores of this species.

Even the elliptical spore shape is unusual, characterizing both *Schistostega* (Figure 42) and the **Splachnaceae**. This shape increases the surface area relative to volume, making attachment easier. Demidova and Filin (1994) have suggested that the light green color of the bulk of spores contrast to the deeply colored ones near the top of the capsule in this species and **Splachnaceae**. They suggest that these light-colored spores would also help attract insects. The autoicous sexual condition (but with separate male and female plants originating from the same protonema and thus from one spore) insures that both sexes will be available (Ignatov & Ignatova 2001). [Note that many bryologists consider this a dioicous condition because the male and female shoots are different; whichever interpretation or term is used, this presents a special case.]

Muscidae and Dung Mosses

The same nomenclatural problem of separate sexes arising from one protonema exists for *Splachnum rubrum* (Figure 43) and *S. luteum* (Figure 44). The family **Splachnaceae**, discussed also in the chapter on nutrients and Terrestrial Diptera, is the only other group of bryophytes considered to be specially adapted for animal dispersal. The oldest report seems to be that of Bryhn (1897), reporting that flies visited *Splachnum rubrum* (Figure 43) and carried the spores to fresh dung. Wettstein (1921) expanded on this observation, verifying dispersal by flies in additional species in the family. Since then, A Koponen, T. Koponen, Cameron, and Marino, among others, have studied this fascinating family extensively, demonstrating not only that flies carry the spores, but determining the attractants.

Among the 73 species in this family, approximately half are **entomophilous**, being dispersed by flies (Diptera) (Erlanson 1930; Koponen & Koponen 1978; Goffinet *et al.* 2004; Marino *et al.* 2009). These same species are **coprophilous**, growing on feces or carrion. Their capsules are often brightly colored and are known to attract flies through their scent, which typically mimics that of decaying organic matter. The relationship between the fly and the moss is typically species-specific, with the capsules producing a unique odor as its attractant. Furthermore, it is the sporophytes that produce the odors (Erlanson 1930; Pyysalo *et al.* 1978, 1983; Marino *et al.* 2009), with the gametophytes being nearly odorless. Interestingly, there was an inverse relationship between the size of the **hypophysis** and the strength of the odor (Marino *et al.* 2009), but perhaps this is an energy tradeoff.

In this family, the peculiar odor attracts the flies that subsequently walk about on the capsules and the spreading **hypophysis** (Figure 1), getting sticky spores (Figure 45) on their bodies, as in *Schistostega*. The flies are usually

attracted to both the dung substrate and the odor of the moss capsules. After investigating the capsules, the flies then travel to other dung, attracted to the odor of the wet dung, and deposit some of the spores as they wander about on the dung.



Figure 43. Capsules of *Splachnum rubrum*, showing the broadly expanded, umbrella-like hypophysis under the capsule. Flies are attracted to the iridescent red color and the odor, with the hypophysis providing a landing platform. Photo by Janice Glime.



Figure 44. *Splachnum luteum* with one of its fly dispersers sitting on the hypophysis. Photo from Biopix, through Creative Commons.

So why should such an elegant moss choose to live on something as unpleasant to humans as dung, and nowhere else? There seems to be no simple answer, so let's examine the facts. This parasol, modified in various ways among the species, is sterile tissue of the sporophyte. Perched atop the umbrella, like the knob to which the spokes of a wheel would be attached, is the capsule, housing the spores. The teeth differ in structure from those of most mosses (Koponen 1978, 1982) and are reflexed at maturity, exposing an open tiny canister of spores (Figure 45).



Figure 45. Capsule of *Splachnum ampullaceum* showing sticky spores with part of expanded **hypophysis** at base. Photo by Janice Glime.

This greatly expanded sterile tissue is the **hypophysis**, concealing a spongy tissue similar to a maple tree's mesophyll. The hypophysis itself is generally brightly colored in *Splachnum*, although somewhat more ordinary in other genera, and provides a landing platform for flies. In *Splachnum ampullaceum* (Figure 46) it is yellow to deep pink, and the plants are so crowded that if the colors don't attract your attention, the sheer numbers will. This of course also amplifies the odor. In *Splachnum rubrum* (Figure 43), the hypophysis is an iridescent purple-red, and I have to wonder if it reflects UV light, visible to some Diptera (Bishop 1974; Gerry *et al.* 2009), but not to us.

By this time, the dung is old and dry, emitting no more odor than the soil beneath, so it is not likely to attract would-be dispersers. However, since the moss has a "perfume" of its own (Erlanson 1930), emitting the unpleasantness of rotting food, sour or musty, from its hypophysis, it attracts the flies. Although these odors are generally faint to our insensitive noses, to a fly they are a virtual invitation. Steere (1958) describes some of the odors. *Tetraplodon* (Figure 50) smells of a strong acetic ester, *Splachnum sphaericum* (Figure 47) of lactic acid, and *S. luteum* (Figure 44) of a butyl compound. These chemicals (Table 2) include volatile octane derivatives and organic acids such as acetic, propionic, and butyric acids that are concentrated in the hypophysis (Koponen 1990).

When the capsule is moist, the columella, with a swollen end, serves as a plug after the operculum is shed. But on a dry day, the capsule contracts and the columella extrudes from the capsule, carrying upward with it clumps of spores exposed to the world. Instead of travelling by wind as individuals, typical of most other mosses, the spores of this moss clump together like the pollen of an

orchid, and apparently to the same advantage. They are picked up inadvertently on the hairs of flies (Koponen 1990; Eriksson 1992) exploring the odor and seeking reward. Once leaving the lure of the capsule, the fly, less discerning than a bee, is likely to be attracted to the odor of fresh dung, and hence carries the clumps of spores to their new home. But the story does not end there. It seems that the fly can even gain an advantage that insures its greater success. Scatophagids, the most frequent and effective of fly visitors, reputedly have greater copulatory success after visiting these mosses (Cameron & Wyatt 1986) – an aphrodisiac for flies!



Figure 46. *Splachnum ampullaceum* in southern Europe, showing the high density of sporophytes. Photo by Michael Lüth, with permission.

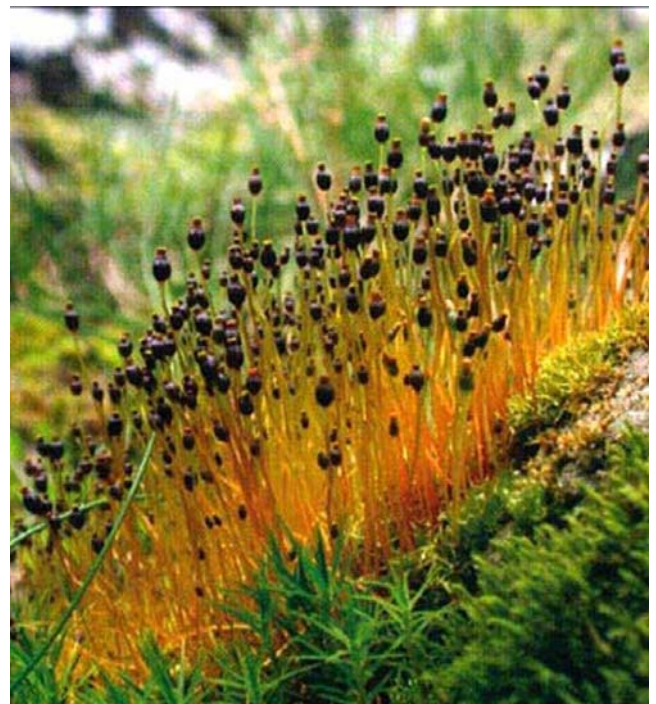


Figure 47. *Splachnum sphaericum* capsules, exhibiting a density that intensifies the lactic acid odor. Photo through Creative Commons.

Diversification of Spore Dispersal Strategy

The fly assemblages differ among individuals and among clumps of the **Splachnaceae** species. Koponen and Koponen (1978) experimented with attraction to **Splachnaceae** in Finland and demonstrated that different combinations of *Poliaetes lardarius* (Figure 48) and other dung flies were attracted to sticky traps baited with hidden sporophytes of *Splachnum ampullaceum* (Figure 46), *S. vasculosum* (Figure 49), and *Tetraplodon mnioides* (Figure 50). Marino (1991a) studied **sympatric** (having overlapping distributions) moss assemblages in central Alberta, Canada. Each moss species attracted 10-17 spore-carrying fly species, but visiting fly species assemblages differed by 77-92% among **Splachnaceae** species (Table 1). Furthermore, the Diptera species captured on the dung were less diverse than those captured from the capsules of the mosses (Marino 1988; 1991b). Marino (1991a) concluded that species-specific recruitment of fly guilds appears to result from differences in attraction to sporophytes through distinct odors created by the moss (especially the capsules), visual cues, or combinations of these.



Figure 48. *Poliaetes lardarius* side view, a dung fly attracted to *Splachnum ampullaceum*. Photo by Richard Bartz, through Wikipedia Commons.

Table 1. Mean (± 1 S.D.) number of spores ($\times 10^3$) carried by fly species trapped on 4 species of mosses in a trapping experiment at Ft. Assiniboine, Alberta. The number of flies carrying spores is shown in parentheses. Fly species in which only a single individual carried spores are not shown (Marino 1991b).

Fly Species	Moss species			
	<i>Tetraplodon angustatus</i>	<i>Tetraplodon mnioides</i>	<i>Splachnum ampullaceum</i>	<i>Splachnum luteum</i>
<i>Eudasyphora cyanocolor</i> Zett.	74 \pm 100 (13)	29 \pm 17 (10)		24 \pm 30 (2)
<i>Helina cothurnata</i> Rondani	52 \pm 39 (11)			
<i>Phormia terrae-novae</i> R.D.	16 \pm 5.3 (2)	20 \pm 20 (9)		
<i>Scatophaga furcata</i> Say	26 \pm 27 (6)		32 \pm 22 (6)	16 \pm 24 (9)
<i>Calliphora vomitoria</i> L.		46 \pm 50 (11)	29 \pm 12 (3)	16 \pm 13 (4)
<i>Pegoplata patellans</i> Pand.			23 \pm 19 (26)	14 \pm 14 (18)
<i>Phormia regina</i> Meigen		42 \pm 50 (4)		
<i>Ravinia</i> sp. 1		6.2 \pm 1.8 (6)		12 \pm 9.1 (16)
<i>Sepsis</i> spp.	5.8 \pm 3.8 (3)			
<i>Cynomyopsis cadaverina</i> L.		30 \pm 27 (7)		
<i>Hydrotæ meteorica</i> L.		17 \pm 7.7 (7)		
<i>Muscina assimilis</i> Fallen		20 \pm 8.2 (4)		
<i>Lucilia</i> sp. 1		23 \pm 13 (4)		
<i>Fannia spathiophora</i> Mall.		24 \pm 35 (3)		
<i>Pegohylomyia</i> sp. 1		14 \pm 12 (2)		
<i>Mydaea</i> sp. 1			25 \pm 23 (5)	
<i>Scatophaga suilla</i> Fab.			29 \pm 22 (5)	
<i>Hebecnema nigricolor</i> Fallen			40 \pm 48 (5)	
<i>Hydrotæ militaris</i> L.			45 \pm 65 (3)	
<i>Phaonia curvipes</i> L.			15 \pm 14 (2)	
<i>Polietes orichalceoides</i> Huck.			69 \pm 19 (2)	
<i>Myospila meditabunda</i> Fab.				3.5 \pm 2.2 (5)
<i>Pegoplata nigriscutellata</i> Stein				6.2 \pm 1.8 (2)
<i>Hydrotæ scambus</i> Zett.				3.7 \pm 1.8 (2)
<i>Hylomyza partita</i> Meigen				6.2 \pm 1.8 (2)
Total	(37)	(63)	(59)	(60)

Table 2. Volatiles detected in the hypophysis and urn of five members of **Splachnaceae**. From Koponen *et al.* 1990. Indications for *Aplodon wormskioldii* based on Pyysalo *et al.* 1983.

	<i>Splachnum luteum</i>	<i>Splachnum vasculosum</i>	<i>Splachnum sphaericum</i>	<i>Aplodon wormskioldii</i>	<i>Splachnum rubrum</i>
Octanal	-	-	X	-	X
3-Octanone	X	-	X	-	-
3-Octanol	-	X	X	X	-
Trans-2-octenal	-	X	X	X	-
1-Octen-3-ol	X	X	X	X	X
1-Octenol	X	X	X	X	-
2-Octen-1-ol	-	X	X	-	-
2-Octenol	-	-	X	-	-
2-Ethyl-hexanal	-	-	X	-	-
Phenylacetylene	-	-	X	X	-
Benzyl alcohol	-	-	X	-	-
Phenole	X	-	X	-	X
Cyclohexycarboxylic acid	-	X	-	-	-
Phenethyl alcohol (2-phenyl ethanol)	-	-	-	-	X
Phenylacetic acid	-	X	X	X	X
Acetic acid	-	-	X	X	-
Propionic acid	-	-	X	X	-
Butyric acid	-	-	X	X	-
Valeric acid	-	-	X	X	-
Caproic acid	-	-	X	X	-
Benzoic acid	-	-	X	X	-
Phenylacetic acid	-	-	X	X	-
Palmitic acid	-	-	X	X	X



Figure 49. *Splachnum vasculosum* capsules and male splash platforms. Photo by Dick Haaksma, with permission.

Cameron and Wyatt (1986) studied dispersal for *Splachnum ampullaceum* (Figure 46), *S. rubrum* (Figure 43), *S. sphaericum* (Figure 47), *S. vasculosum* (Figure 49), and *Tetraplodon mnioides* (Figure 50) and found that the fly family Scatophagidae (*Scatophaga*; Figure 51) was both the most frequent and most effective visitor to the moss colonies. Other visitors included *Delia* (Anthomyiidae), *Myospila* (Muscidae; Figure 52), and *Eudasyphora* (as *Pyrellia*; Muscidae; Figure 53). They further demonstrated that wind is not an effective dispersal agent for these species.



Figure 50. *Tetraplodon mnioides* capsules. Photo by Zen Iwatsuki, with permission.



Figure 51. *Scatophaga stercoraria*, member of a genus that visits **Splachnaceae** capsules. Photo by Luc Viatour <www.Lucnix.be>, through Creative Commons.



Figure 52. *Myospila mediatubunda*, member of a genus that visits **Splachnaceae**. Photo by Valter Jacinto, through Creative Commons.



Figure 53. *Eudasyphora cyanicolor*, a carrion fly. Photo by Tristram Brelstaff, through Creative Commons.

Troilo and Cameron (1981) consider the transport of spores in the *Splachnum ampullaceum* (Figure 46) by flies [*Eudasyphora* (as *Pyrellia*) *cyanicolor* (Figure 53)] to be passive. This fly species oviposits on carrion, but it will use dung when carrion is not available, whereas *S. ampullaceum* grows almost exclusively on dung. The moss capsules attract them, and if they are chased away, they quickly return. The capsule is adapted by its bright colors, expanded hypophysis that serves both to attract and as a landing platform, a dung-like odor, teeth that extend outward, and a shrinking capsule that forces the adhesive spores outward. Cameron and Troilo (1982) added to this story by documenting that landing by *Eudasyphora cyanicolor* flies demonstrated a 20-fold preference for yellow-colored disks over blue or red disks placed among sporophytes of *S. ampullaceum* in Michigan, USA, suggesting the spore dispersal may not be passive after all. In fact, they never visited the red disks. This is an interesting observation and begs further investigation. Flies are typically attracted to red (don't wear red in mosquito or blackfly season!). And *S. ampullaceum* typically has a mix of yellow and pinkish red capsules (Figure 1). On the other hand, pink flowers do not usually attract flies.

The most activity of *Eudasyphora* (Muscidae; Figure 53) on the capsules was on warm days when the odors were strongest (Troilo & Cameron 1981). The moss is a successful odor mimic, as demonstrated by fly visits that equalled those to carrion and exceeded those to a protein source or fly medium (Figure 54). But once there, the visit to the moss capsule was significantly shorter than visits to carrion or protein substitute. Moreover, the flies never exhibited feeding behavior on the capsules, only sampling behavior. Troilo and Cameron consider this to be a **commensal** relationship in which the moss benefits from dispersal but the flies are neither benefitted nor harmed. One could argue that the moss is being a parasite by taking energy from the flies and using it for dispersal while providing nothing in return, but others have argued that the flies may get the benefit of increased mating opportunity.

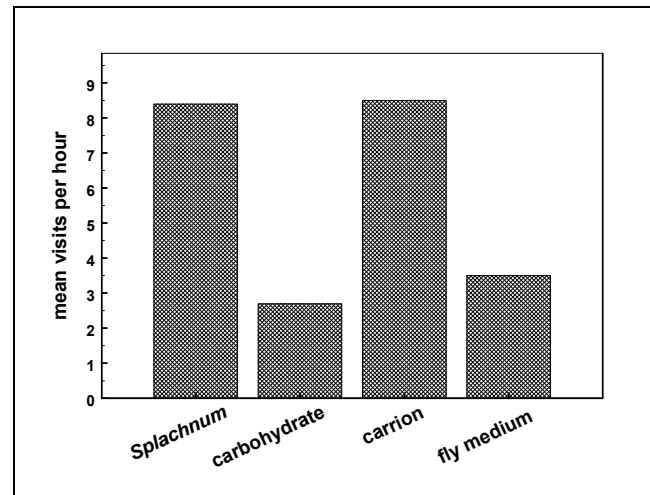


Figure 54. Mean number of visits by the carrion fly *Eudasyphora cyanicolor* (Figure 53) on *Splachnum ampullaceum* (Figure 46) and three nutritional substrates. Note that there was no evidence of feeding on *S. ampullaceum*. Graph based on table from Troilo & Cameron 1981.

Many of the fly species associated with the **Splachnaceae** studied by Marino (1991b) are anthomyiids. By mimicking the flower and odor cues typically used by the adult **Anthomyiidae**, a family with seed predators and pollinators, the mosses have achieved what appears to be a very effective means of spore dispersal.

This very targeted means of dispersal may be a tradeoff between energy needed for attraction and that needed for spore production (Marino 1991a). These species have fewer spores **and** smaller spores than most mosses. This high energy requirement may account for the evolution from a specialist such as these entomophilous species to the generalist strategy of the coprophilous species such as *Tetraplodon paradoxus* (Figure 55), and the two *Voitia* species (**Voitioideae**; Figure 56) that lack sporangial dehiscence. In *Tayloria* (Figure 57), both anemophilous and entomophilous species exist.



Figure 55. *Tetraplodon paradoxus*, a species with indehiscent capsules. Photo by Michael Lüth, with permission.



Figure 56. *Voitia nivalis* with capsules. Photo by Michael Lüth, with permission.

It appears that the dung habitat may provide another significant role. One advantage to this dispersal type is that it ensures that both male and female spores will arrive at the same site. In populations of *Tayloria tenuis* (Figure 57) on cattle droppings in the Eastern Pyrenees, the protonemata are at first the only conspicuous stage (Lloret 1991). The plants are clustered and despite high mortality, the entire dung substrate is soon covered with protonemata. Within 1-2 years the leafy plants develop and ultimately produce capsules. These capsules are often numerous, as seen in *Splachnum ampullaceum* (Figure 46). This is in part due to the female:male ratio of 2:1, at least in the *Splachnum* species [*S. ampullaceum* (Figure 46), *S. sphaericum* (Figure 47), *S. rubrum* (Figure 43)] of Isle Royale, Michigan, USA (Cameron & Wyatt 1990). But in experiments, environmental conditions can alter this ratio, with low light, pH, and nutrients favoring the production of males.

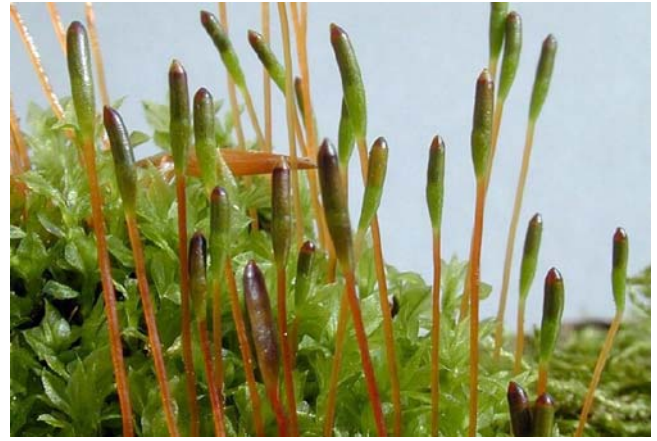


Figure 57. *Tayloria tenuis* with capsules, a species that grows on dung. Photo by Michael Lüth, with permission.

In *Splachnum ampullaceum* (Figure 46), males and females can arise from the same protonema, ruling out any bias in dispersal of spores. For this high degree of fertilization success, dispersal of the sperm to the female benefits from the density of the plants. Cameron and Wyatt (1990) found that the average sperm dispersal distance is less than 5 mm. This proliferation of sporophytes is reminiscent of the Asteraceae, acting as a single unit through the clumping of so many capsules. Furthermore, the early period of establishment has served to eliminate weak genotypes among the protonemata, although there is no guarantee that these same weaknesses would occur among the leafy plants.

As the capsules mature, that moist and smelly dung that once attracted the flies becomes dry and looks more like a cardboard Frisbee, or in the case of moose dung, like a clump of well-done toasted marshmallows. Nevertheless, once spores are sent upon their way, the remaining plants are soon covered by larger pleurocarpous mosses that are typical of the forest soil. This is an ephemeral habitat for the **Splachnaceae**.

All of this attraction is costly, requiring energy to produce the hypophysis and make volatile attractants. To maintain this, the mosses are able to access the higher concentrations of N, P, and Ca that occurs in dung (Webster 1987). Meanwhile, most other mosses typically die in areas with such high nitrogen concentrations resulting from manuring (Geissler 1982). There have also been suggestions that the growth of the protonemata may be promoted by substances such as Gibberellic Acid produced by accompanying fungi (Von Maltzahn & MacQuarrie 1958; Vaarama & Tarén 1959).

Cameron and Wyatt (1986) have suggested that the **Splachnaceae** requirements for dung may actually be a requirement for their fly dispersers, and the flies travel from one dung heap to another. There seems to be an interesting correlation between means of dispersal and substrate that supports this hypothesis. As noted earlier, all of the **entomochorous** (i.e. requiring insect dispersal) species are also **coprophilous** (living on dung or corpses); the **anemochorous** (wind-dispersed) species are **humicolous** or epiphytic (Goffinet & Shaw 2002). In the subfamily **Voitioideae**, three taxa are coprophilous but cleistocarpous (capsule not opening), lacking a peristome and dispersing spores only after the sporangial wall disintegrates.

Flies are not restricted to landing on dung, to any particular moss species, or to any particular habitat (Marino 1986), so this diverse behavior would seem to limit successful dispersal. Nevertheless, spore success is typically very low among mosses, so even this hit-or-miss mechanism may be better than wind dispersal. And certainly it must be for these sticky spores.

In summary, Koponen (1990) considers three categories of adaptations of bryophytes for entomophily in the **Splachnaceae**:

- adaptations to a substrate of animal origin
- morphological adaptations
- chemical adaptations

In support of this, Koponen cites *Splachnum* (Figure 49) and the entomophilous species of *Tayloria* (Figure 61-Figure 62) as being restricted to the dung of herbivorous mammals. *Tetraplodon* (Figure 58-Figure 59) grows on skeletal remains, antlers, stomach pellets of predatory birds, or on dung. The entomophilous *Aplodon wormskioldii* (Figure 60) grows on corpses, on caribou (reindeer) dung, bones and antlers, on owl pellets, or on enriched gravel.



Figure 58. *Tetraplodon angustatus* with capsules on caribou antler at Jasper, Canada. Photo by Janice Glime.

Those of us in the Northern Hemisphere are familiar with this fascinating family of mosses largely because of their ability to attract flies, but in the Southern Hemisphere, such attraction does not exist, or does it?! Mighell (2011) investigated *Tayloria mirabilis* (Figure 61-Figure 62), a South American endemic, because it had been suspected of having fly dispersal. They trapped 218 flies over the plants on dung and found that 63 of them had spores of *T. mirabilis*. The flies comprised seven species from Muscidae and Calliphoridae. Furthermore, germination of the transported spores were 46.7% successful; identity of the spores was verified by DNA analysis. This example becomes more interesting when we realize that the plants (and flies) are associated with more than one kind of forest dung and that all the current large forest mammals there are exotic! Rapid evolution or pre-adaptation?



Figure 59. *Tetraplodon angustatus* with capsules on caribou skull at Jasper, Canada. Photo by Janice Glime.



Figure 60. *Aplodon wormskioldii* with capsules in Svalbard. Photo by Michael Lüth, with permission.



Figure 61. *Tayloria mirabilis* capsules, a species that attracts flies in the Southern Hemisphere. Photo by Jan-Peter Frahm, with permission.



Figure 62. *Tayloria mirabilis* capsules and fly near Cape Horn, Chile. Note the spores on the front leg and around the eye. Photo by Adam Wilson, through NYBG public domain.

In the same year, Jofré *et al.* (2011) reported a second example of fly-attracting Splachnaceae in the Southern Hemisphere. This time, it was *Tayloria dubyi* (Figure 63) growing on bird dung in the subAntarctic region of Cape Horn, Chile. The bird dung appears to be exclusively that of the Snow Goose *Chloephaga picta* (Figure 64). When Jofré Acevedo (2008) germinated the spores in the lab, they grew much better on snow goose dung than on horse or cattle dung. *Tayloria dubyi* releases its spores in the same months as the highest activity of Diptera (Jofré *et al.* (2010). Based on these findings, Jofré *et al.* (2011) trapped 64 flies, comprised of *Palpibracus chilensis* (Muscidae), *Dasyuromyia* sp. (Tachinidae), and an unidentified member of the Sarcophagidae, in traps above the sporophytes, but no flies appeared in traps above nearby *Sphagnum*, suggesting that *Tayloria dubyi* also attracts the flies.

Once we understood that flies were indeed attracted to the capsules of the Splachnaceae, not just (if at all) to the odors of the dung, work began to elucidate the attracting compounds. Koponen *et al.* (1990) identified 23 compounds in the hypophysis and urn among five Splachnaceae, demonstrating that the individual species were often unique. Data from the setae are not included here. The only volatile compound in the substratum was benzaldehyde, a compound not found in the capsules or setae.



Figure 63. *Tayloria dubyi* capsules, a Southern Hemisphere species of Splachnaceae that apparently attracts flies. Photo by Jocelyn Jofré., with permission.



Figure 64. *Chloephaga picta* (Snow Goose), potential bryophyte dispersal agents through the gut as well as feet and feathers. Photo by Fabien Dany <www.fabiendany.com>, through Creative Commons.

Molluscs

Could it be that slugs that consume capsules (Figure 65) do indeed carry spores to new locations? But alas, a slug by its very nature is slow, and such dispersal would not move the spores very far from home. Nevertheless, consumption can result in movement of spores to a new location, even if not very far away. But can they live?



Figure 65. Slug preying on capsules of *Leucolepis acanthoneuron*. Photo from Botany website, UBC, with permission.

Boch *et al.* (2013) tested the possibility that slugs could eat bryophyte spores, and that the spores could subsequently germinate. They fed capsules of four bryophyte species to three slug species. Overall,

approximately in half (51.3%) all 117 bryophyte samples fed to slugs, representing four bryophyte species [*Bryum pallescens* (Figure 66), *Funaria hygrometrica* (Figure 109), *Leptobryum pyriforme* (Figure 67), *Pellia endiviifolia* (Figure 68)], spores did germinate from feces. It is interesting that there was no difference between bryophyte species, but there were large differences among the three slug species (Figure 69). Spores from the feces of the slugs *Arion lusitanicus* (Figure 70) and *A. rufus* (Figure 71) had 76% and 74% success, respectively. Those from *Limax cinereoniger* (Figure 72), on the other hand, were only 12.9% successful. This mechanism would enhance the population size by moving spores away from the parent, but at the same time being more likely than wind dispersal to deposit them in places where they can grow successfully. Türke *et al.* (2013) found that slugs could transport seeds in the gut for 5 m, giving us an estimate of potential bryophyte dispersal distance.



Figure 66. *Bryum pallescens* with capsules, a species for which spores can be dispersed by slugs. Photo by David Holyoak, with permission.



Figure 67. *Leptobryum pyriforme* with capsules, a species for which spores can be dispersed by slugs. Photo by Michael Lüth, with permission.



Figure 68. *Pellia endiviifolia* males with reddish antheridial cavities and females in center. David Holyoak, with permission.

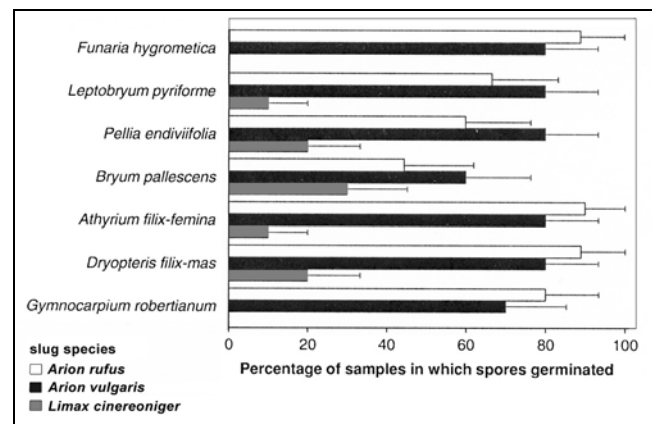


Figure 69. Germination percentages of bryophyte spores from feces of three species of slugs. Redrawn from Boch *et al.* 2013.



Figure 70. *Arion lusitanicus*, a species that disperses bryophyte spores through its feces. Photo by Håkan Svensson, through Wikimedia Commons.

In an experiment to determine success of spores that travelled through the digestive tract of slugs (*Arion* spp.; Figure 70), all plates containing eaten spores of *Mnium hornum* (Figure 73) and *Brachythecium rutabulum* (Figure 74) produced shoots, whereas only 80% of the plates with uneaten mature *Mnium hornum* spores and

70% of those with uneaten *Brachythecium rutabulum* spores produced shoots (Davidson 1989). Furthermore, the eaten spores showed little infection, suggesting some antibiotic property acquired from the digestive tract. Nitrogen, secreted in mucus and disposed in feces, may have enhanced the success of these spores.



Figure 71. *Arion rufus*, a species that disperse bryophyte spores through its feces. Photo by Walter Siegmund, through Wikimedia Commons.



Figure 72. *Limax cinereoniger*, a species in which most bryophyte spores died on the way through the digestive tract. Photo by Teemu Mäki, through Creative Commons.



Figure 73. *Mnium hornum*, a species whose spores are eaten by slugs in southern Europe. Photo by Michael Lüth, with permission.



Figure 74. *Brachythecium rutabulum* with capsules. Spores of this species are eaten by slugs. Photo by David Holyoak, with permission.

Using 11 species of mosses and 1 of liverworts, Boch *et al.* (2014) supported the concept that slugs can increase bryophyte establishment. They demonstrated that through their herbivory, the slugs reduce light competition, permitting a greater diversity of bryophytes to establish. Furthermore, the spores they ingest are able to germinate after passing through the digestive tract of the slug (**endozoochory**). After 21 days in an experimental setup, bryophyte cover was 2.8 times as high in enclosures with slugs that had previously been fed sporophytes when compared to enclosures with slugs that had not been fed sporophytes or with no slugs.

After 21 days the bryophyte cover was on average 2.8 times higher (3.9% versus 1.4%) and after eight months the bryophyte species richness 2.6 times higher (5.8 versus 2.2) in enclosures containing slugs previously fed with bryophyte sporophytes than in the other treatments. After 8 months, the increased vascular plant cover reduced the bryophyte diversity. Enclosures that had no seed sowing had 1.6 times as many bryophyte species compared to those receiving seeds.

But if we look further, we find that long distance travel by slugs and snails is indeed a possibility. Malone (1965) determined that fresh-water snails were able to attach to the feed of the killdeer (*Charadrius vociferus*) and travel there for sufficient time to accomplish overland dispersal, remaining alive. Adults of the snail *Lymnaea emarginata* could survive at least 14 hours. It is likely that other birds, both aquatic and terrestrial, could carry snails as well, providing considerable time for dispersal and making long-distance dispersal possible. And how long might the spores survive in a snail or slug eaten by a bird? Will those spores also be viable?

Fish

The ability of fish to transport bryophytes remains to be demonstrated. My student experimented with rainbow trout, known to strike at almost anything, to see if they would eat mosses in their attempts to remove aquatic insects. The student was unable to get the fish to attack the moving moss or eat it to get at insects. Finally, in desperation, he force fed it *Fontinalis duriaei* (Figure 75). Then he waited to collect the feces. The moss did appear in a cylindrical package of feces. It emerged in bright green

color and looked healthy. We put it in a jar of stream water from which the moss had been collected, kept it cold, and waited expectantly. Alas, the second day the *Fontinalis* was pale and appeared to be dead. No growth ever ensued.



Figure 75. *Fontinalis duriaei*, a species refused by rainbow trout and that does not survive in feces from force-fed fish. Photo by Michael Lüth, with permission.

Birds

Until recently, birds were barely considered as dispersers of bryophytes. Ducks are dispersers (Proctor 1959), but we have no idea how important they are. Spores of *Riella* (Figure 76; Tenge 1959) pass through the digestive tract of Mallards (*Anas platyrhynchos*; Figure 77) and remain viable (Proctor 1961). Assuming a mean residence time similar to that of seeds, which is about 7.5 hours, a migrating Mallard could move spores of this liverwort 20-30 km easily, and at times up to 1,400 km (Mueller & van der Valk 2002). It could, but does it?



Figure 76. *Riella cossoniana* showing sporangia (dark spheres) that can be dispersed by ducks. Photo by Jan-Peter Frahm, with permission.



Figure 77. *Anas platyrhynchos* (Mallards) female and male, potential dispersal vectors for aquatic bryophyte diaspores. Photo by Richard Bartz, through Wikimedia Commons.

Proctor (1961) suggested that the rarity of *Riella americana* may result from very specialized dispersal. Griffin (1961) found a large population of this species in a playa lake in Texas, USA, where its population measured 60 cm in width and approximately 1.7 km long. The production of gemmae may contribute to such large populations (Studhalter 1931). He examined 25 nearby similar lakes within a 25 km radius and could find no trace of the liverwort.

Following these observations, Proctor (1961) experimented with the possibility that this liverwort was dispersed by ducks. He used three Mallard ducks (*Anas platyrhynchos*; Figure 77) that had been used previously for similar experiments with the alga *Chara*. These ducks were provided with approximately 57 liters of the *Riella americana*, which they readily ate. The plants had abundant sporophytes with what appeared to be mature brown spores. The feces were collected after approximately 1 hour and handled according to treatments in Table 3. The feces contained many spores that had separated from their masses, no intact sporophytes, and thallus fragments that were clearly dead. Feces were collected for three days, and on the third day they were separated by individual duck. It was interesting that one male and one female had numerous spores in their feces, but the second female had none! Germination success ranged from 0 - >30%.

Table 3. Various storage effects on germination of *Riella americana* spores collected from Mallard duck feces. Germination follows 60 days of treatment, then 14 days of inoculation at 24°C on sterile tubes of soil and water in light. + = <10% germination; ++ = 10-30% germination; +++ = >30% germination; - = no germination; blank = not enough spores for test. Based on Proctor 1961.

	day 1	day 2	day 3 male	day 3 female
ice (-10°C)	++	+		
water at 1°C	+++	+++	+++	+++
water at 24°C	+++	+++	+	+
water at 37°C	+++	+++	+++	+++
dried, stored at -10°C	-	+	++	++
dried, stored at 24°C	+++	+++		
dried, stored at 37°C	+++	+++		

Proctor (1961) found that the spores of *Riella americana* (Figure 78) from feces germinated as well as fresh spores (not eaten). These spores mature at the time ducks and other water birds are migrating through that area of Texas in early autumn, so their transport through water bird guts is quite possible. Proctor (1961) suggests that many spores can be transported in the gut for up to 80 km. Furthermore, as already suggested by Studhalter (1932) and Persson and Imam (1960), external transport of spores and even fragments on feathers, beaks, and feet is a likely possibility. This notion is supported by the presence of spines on the spores (Figure 78) (Studhalter 1933). Furthermore, the spores have sufficient longevity to survive in muds or on birds (3 years for *R. americana*, 12 years for *R. capensis*). And it is possible that some remain in tetrads during dispersal, further protecting them from UV light and desiccation. Considering these dispersal potentials, it seems that something else must explain the rarity. Perhaps there is too much herbivory before they can become established? Could timing be important to avoid herbivory during establishment?

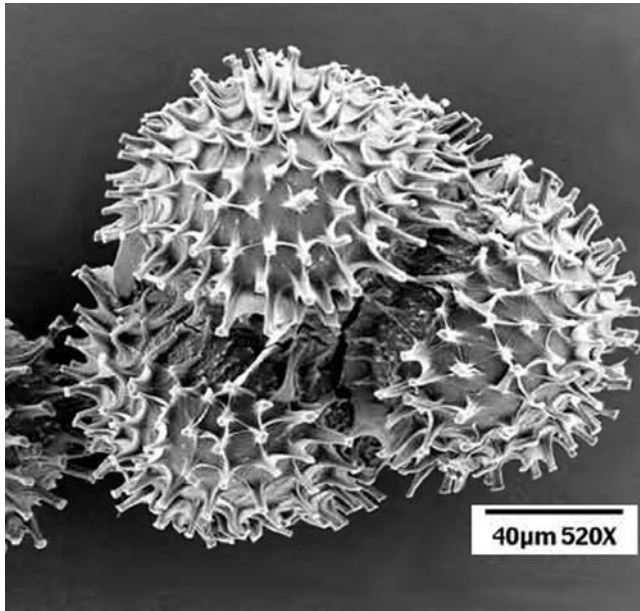


Figure 78. *Riella americana* spore tetrad SEM, exhibiting spines that could attach to feathers of ducks. Photo by William T. Doyle, with permission.

Riella is not the only bryophyte to experience dispersal by ducks. Des Callaghan (Bryonet 26 August 2016) reported that his friend had sent him a moss shoot grown from a fragment in a Mallard dropping (*Anas platyrhynchos* (Figure 77). This turned out to be the moss *Didymodon insulanus* (Figure 79).

Recent studies have revealed that other birds may also be dispersers. Using fecal samples from the herbivorous Upland Goose (*Chloephaga picta*; Figure 64) and White-bellied Seedsnipe (*Attagis malouinus*; Figure 80), Behling *et al.* found vegetative diaspores, including various moss fragments. Experiments continue to determine their viability. *Attagis malouinus* feeds among the low vegetation, sits among the mosses, and may even spread its wings across the mosses in the tundra, affording numerous opportunities for snagging the local bryophytes.



Figure 79. *Didymodon insulanus*, a species whose fragments survived the digestive tract of a Mallard. Photo by David T. Holyoak, with permission.



Figure 80. *Attagis malouinus*, a species that carries bryophyte propagules among its feathers. Photo by Jacob Wijpkema <jacob.wijpkema@gmail.com> & Tini Dijk <tini.wijpkema@gmail.com>, with permission.

Just imagine how far diaspores might travel by **ecto-zoochory** (on the outside of an animal) among the bird plumage. We know birds survive airplane travel, so bird travel is not a stretch. And the idea is not so far-fetched when we consider the number of bipolar species of bryophytes and the number of birds that travel those same distances from Arctic to the Antarctic. Lewis *et al.* (2014) developed a method to screen feathers of wild birds that travelled these long distances in their annual migrations. They concluded that the entire flock of migrating birds may leave their northern breeding grounds carrying potentially viable propagules, providing opportunities for dispersal everywhere they land to feed or rest.

Szepesfalvy (1955 in Schuster 1966) found *Riccia frostii* (Figure 81) concentrated along goose paths in central Hungary and suggested that the spores of this species were distributed on feet and beaks of these domestic geese. And we cannot, without testing it, eliminate the possibility of distribution of spores in feces (Figure 82), although it would require having the geese eat something that ate the spores or carried them on its surface. Szepesfalvy also suggested that spores and overwintering thallus pieces of *Riccia bischoffii* var. *ciliifera* (Figure 83)

are distributed by pheasants, but both of these suggestions are based on circumstantial evidence and the correlation may be one of habitat rather than dispersal agent. Furthermore, these birds are surely not the only animals to frequent these paths. Szepesfalvy also suggested a relationship between presence of hares and distribution of *Oxymitra paleacea* (Figure 84), but this meets the same problem of verification.



Figure 81. *Riccia frostii*, a liverwort that can concentrate along goose paths, presumably due to having the geese spread the spores. Photo by Rosemary Taylor, with permission.



Figure 82. Canada Goose (*Branta canadensis*) dung at a wildlife station, Ohio, USA – a potential dispersal mechanism. Photo by Janice Glime.



Figure 83. *Riccia bischoffii* var. *ciliifera*, a species with overwintering fragments that may be dispersed by geese. Photo by Jan-Peter Frahm, with permission.



Figure 84. *Oxymitra paleacea*. Photo by EncycloPetey, through Creative Commons.

Brandon Stone reported to Bryonet (9 April 2003) that he found sporophytes of the moss *Pyrrhobryum spiniforme* (Figure 85) in a bird's nest at 1300 m on Moloka'i in Hawai'i. A bird expert told him the bird was most likely not a native bird. Transport of such sporophytes at the right stage could contribute to dispersal over more than the normal range of dispersal from capsules on the ground.



Figure 85. *Pyrrhobryum spiniforme* showing sporophyte that is used in making birds' nests in Hawaii. Photo by Michael Lüth, with permission.

Several birds frequent upturned roots where *Schistostega pennata* (Figure 86) is common in Russia, and there is evidence that these may transmit spores (Ignatov & Ignatova 2001). The tiny Winter Wren (*Troglodytes troglodytes*; Figure 87-Figure 88) visits upturned roots to look for insects and sometimes nests there. Above one nest near a convenient perch, there were protonemata of *S. pennata*, suggesting they may have arrived as spores on the birds.

A more convincing case of bird dispersal is that of the cock *Tetrastes bonasia* (Hazel Grouse; Figure 89) (Ignatov & Ignatova 2001). These large birds take dust baths near the upturned roots. Feathers collected there did have spores of *S. pennata* attached. However, no chloroplasts seemed to be present, so it is unlikely that they were still viable. The birds also help in dispersal of spores by capturing beetles such as *Geotrupes* (Figure 90) with adhering spores and distributing their parts to other locations. Mice and frogs also visited tip-up areas, but there was no direct evidence that they transported spores.



Figure 86. Capsule and seta of *Schistostega pennata*. Note the delicate, white stalk and the sticky spores on the outside of the capsule. Photo with written permission from Misha Ignatov.



Figure 87. *Troglodytes troglodytes* (Winter Wren), known to build nests near good locations for *Schistostega pennata*, possibly transporting spores. Photo by Sonja Kübelbeck, through Wikimedia Commons.



Figure 88. *Troglodytes troglodytes indigenus* on a moss-covered tree from Kuwait, a winter wren that might disperse bryophyte spores to a perch above its nest. Photo by Bob McCaffrey, through Creative Commons.



Figure 89. *Tetrastes bonasia* (Hazel Grouse) transports bryophyte spores and also eats beetles that carry them, but viability of the spores is unknown. Photo by Kallerna, through Wikimedia Commons.



Figure 90. *Geotrupes stercorarius* on moss, a beetle species that can carry spores, then get transported farther when captured by birds. Photo by Thomas Bresson, through Wikimedia Creative Commons.

We have already noted that slugs can carry viable spores in their digestive tracts. Birds eat slugs. Could it be that the spores could survive both digestive tracts? Wada *et al.* (2011) addressed this very question. Japanese land snails are preyed upon by birds, including the Japanese White-eye (*Zosterops japonicus*; Figure 91) and the Brown-eared Bulbul (*Hypsipetes amaurotis*; Figure 92). Of the 119 snails (*Tornatellides boeningi*; Figure 93) fed to Japanese White-eyes and 55 snails fed to Brown-eared Bulbuls, 14.3% and 16.4% of the snails, respectively, passed through the gut alive. For us, the logical next question is whether this provides an additional means of dispersal for bryophyte spores, potentially giving them a free ride to greater distances while being protected from the

bird's digestive system by the snail. Kawakami *et al.* (1965) suggested that it is.



Figure 91. Japanese White-eye (*Zosterops japonicus*). Photo by Ltshears, through Creative Commons.



Figure 92. Brown-eared Bulbul (*Hypsipetes amaurotis*). Photo by Lip Kee Yap, through Wikimedia Commons.



Figure 93. *Tornatellides boeningi*, a species that can pass through bird guts and survive. Photo by Shinichiro Wada, through Creative Commons.

Griffin *et al.* (1982) suggested that *Dendrocryphaea latifolia* may have reached the high Andes of Colombia by wind or birds, but there is no direct evidence to support this.

As Ken Adams suggested on Bryonet (5 March 2013), birds might occasionally be responsible for long-range bryophyte dispersal. Spores could lodge on or among feathers or feet, especially in mud, protecting them from both desiccation and UV light. Michael Richardson (Bryonet 5 March 2013) suggested that this could occur as short hops (stepping stones), with birds depositing spores at resting or feeding points along the way. When those establish, they provide a new and closer source for dispersal to more distant locations. Richardson suggested that gulls might be good vectors because of their need for fresh-water baths and their puddle-hopping behavior. Terry McIntosh (Bryonet 5 March 2013) suggested that birds may account for some of the wide disjunctions in western North America for species that are restricted to open soil in the grassy edges of saline ponds and depressions. This could explain the distribution of such species as *Entosthodon rubiginosus* and *Tortula nevadensis*.

Fife and de Lange (2009) suggested that shearwaters (*Procellariidae*; Figure 96) may have been responsible for transporting propagules of the pan-tropical *Calymperes tenerum* (Figure 94) to the Chatham Islands and Kermadecs off the coast of New Zealand. These fantastic birds fly from Alaska to Australia and other parts in the deep Southern Hemisphere, then back to Alaska each year.



Figure 94. *Calymperes tenerum* with gemmae. Photo by Jan-Peter Frahm, with permission.

Jesús Muñoz (Bryonet 15 March 2013) studied the effects of wind on Cory's Shearwater (*Calonectris diomedea*; Figure 95) migration and suggested that it might be worth investigating those same wind patterns for bryophyte dispersal. Earlier in this chapter I suggested that propagules might follow "wind highways." Could this following be in the protection of the feathers and mud of birds? Felicísimo *et al.* (2008) used a model to show that the Cory's Shearwaters closely follow the "wind highways" that require the least energy to reach their breeding and wintering areas. The Manx Shearwaters (*Puffinus puffinus*; Figure 96) chose a route that was 25% longer, avoiding turbulence on the shortest distance (González-Solís *et al.* 2009). The wind patterns (not the shortest route) drive the shearwaters in their movements and could do the same for bryophytes (Felicísimo *et al.* 2008; González-Solís *et al.* 2009).



Figure 95. *Calonectris diomedea* (Cory's Shearwaters). Photo by Antlewis, through Creative Commons.



Figure 96. Manx Shearwater (*Puffinus puffinus*) in Iceland, a potential bryophyte dispersal agent. Photo by Chiswick Chap, through Creative Commons.

Brent Mishler (Bryonet 5 March 2013) suggested that vegetative fragments could travel in mud on birds' feet as well, and that molecular testing could be used to track such long-distance dispersal. Rob Gradstein (Bryonet 11 March 2013) suggests a less molecular, more challenging approach: 1) capturing migratory birds to look for bryophyte spores, gemmae, and fragments on their feathers, feet, and beaks; 2) flying spores, gemmae, and fragments on birds across long distances to test for germinability of the diaspores after the long trip.

Even feet of terrestrial birds can carry spores, and probably other propagules. Davison (1976) reported finding spores of bryophytes on the feet of the Song Thrush (*Turdus philomelos*; Figure 97) in beechwood in Great Britain, although he considered that these were transported only a short distance.

Even the tiny hummingbird may contribute to long-distance dispersal of bryophytes. Torres-Dowdall *et al.* (2007) reported the use of bryophytes in the construction of nests of the hummingbird called Picaflor Rubi (*Sephanoides sephanioides*; Figure 98-Figure 99) in Chile. Osorio-Zuñiga (2012) later examined the nests of the Picaflor Rubi (also known as Picaflor Chico). He identified *Lophosoria quadripinnata* (a tree fern), appearing as the "garment" in 100% of the nests, and three moss species, all pendent species, that frequently comprised the outside of the nests [*Weymouthia*

cochlearifolia (16.6% of nests) (Figure 100), *W. mollis* (26.6%) (Figure 101), and *Ancistrodes genuflexa* (100%) (Figure 102-Figure 103). These outside mosses all produced sporophytes in both the old and new nests (Figure 106-Figure 108). In addition to these species, old nests also had *Eriodon conostomus* (Figure 104), *Ptychomnion ptychocarpon*, and *Dicranoloma robustum* (Figure 105), all producing sporophytes (Figure 108). For species present in 100% of the nests, the growing heights were 10-18 m above ground and were not the most abundant species in the forest.



Figure 97. Song Thrush (*Turdus philomelos*), a bird known to carry moss spores on its feet. Photo by Taco Meeuwssen, through Wikimedia Commons.

In continuing this study, Osorio-Zuñiga *et al.* (2014) introduced the concept of **synzoochory** for bryophyte dispersal as an intermediate between endo- and ectozoochory. In **synzoochory**, the propagules are deliberately transported, usually by mouth or beak, but without ingestion. These researchers found seven species of mosses were transported this way by the hummingbird *Sephanoides sephanioides* (Figure 98). These likewise were to be used in nests, but the researchers found that the birds were selective, choosing mosses with capsules in greater frequency than their appearance in the habitat. They also preferred the fern *Lophosoria quadripinnata* and the moss *Ancistrodes genuflexa* (Figure 102-Figure 103), with the other mosses [*Weymouthia mollis* (Figure 101), *Weymouthia cochlearifolia* (Figure 100), *Eriodon conostomus* (Figure 104), *Ptychomnion ptychocarpon*, *Dicranoloma robustum* (Figure 105), *Rigodium toxarion*] being minor components. This behavior of the birds gave two opportunities for greater dispersal – first from one tree to another in the beak, then for longer distances for the spores from the elevated position of the nest. In some cases the mosses were elevated from the ground to the nest.



Figure 98. Picaflor Rubi (*Sephaniodes sephaniodes*), a hummingbird that selects mosses for her nest. Photo by Suemili, through Wikimedia Commons.



Figure 99. *Sephaniodes sephaniodes* on moss-constructed nest, looking quite camouflaged. Photo by Diucón, through GNU Free Documentation.



Figure 100. *Weymouthia cochlearifolia*, a pendent moss used in the nests of the Picaflor Rubi. Photo by Juan Larrain, with permission.



Figure 101. *Weymouthia mollis*, a pendent moss that is placed on the outside of the nests of the Picaflor Rubi. Photo by Juan Larrain, with permission.



Figure 102. *Ancistrodes genuflexa*, a pendent moss used in the outside of the nests of the Picaflor Rubi. Photo by Felipe Osorio Zúñiga, with permission.



Figure 103. *Ancistrodes genuflexa* with capsules. Photo by Felipe Osorio Zúñiga, with permission.



Figure 104. *Eriodon conostomus* with capsules. Photo by Juan Larrain, through Creative Commons.



Figure 105. *Dicranoloma robustum*. Photo by Juan Larrain, through Creative Commons.

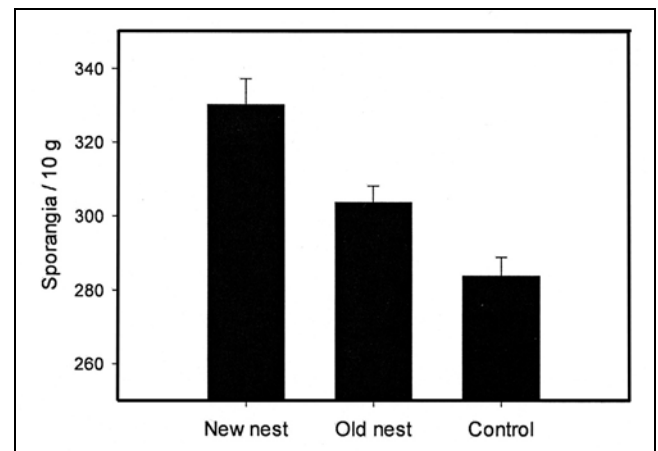


Figure 106. Sporophyte number vs nest age in 10 g of nest mosses for the Picaflor Rubi (*Sephanoides sephaniodes*). Redrawn from Osorio Zúñiga (2012).

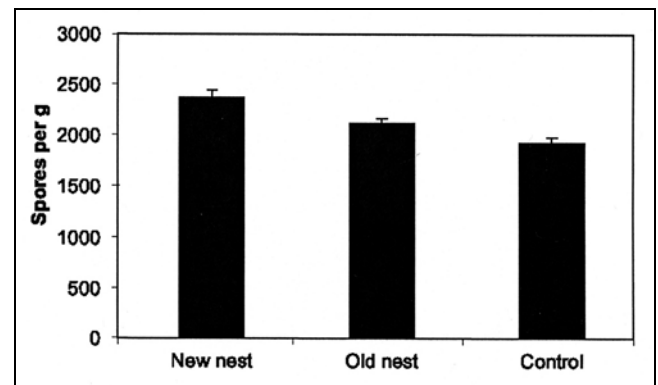


Figure 107. Effect of nest age on spore number per gram of moss in nests of the Picaflor Rubi (*Sephanoides sephaniodes*). Redrawn from Osorio Zúñiga (2012).

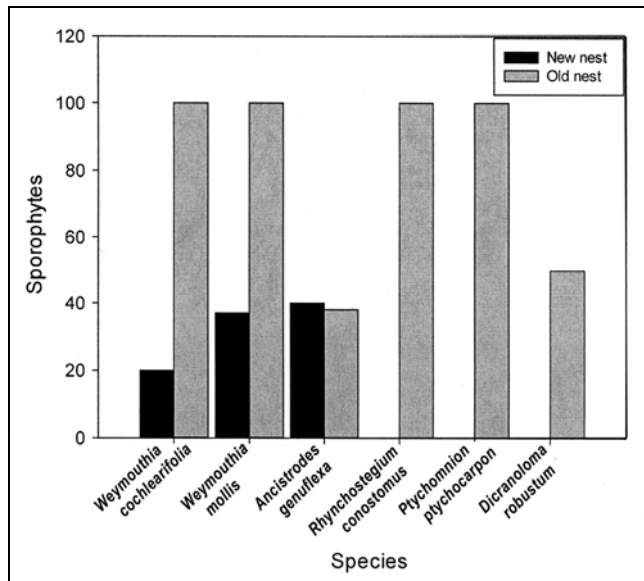


Figure 108. Number of sporophytes compared to nest age for bryophytes in nests of the Picaflor Rubi (*Sephanoides sephanoides*). Redrawn from Osorio Zúñiga 2012.

As noted above, members of the **Splachnaceae** are known for their ability to attract flies that subsequently disperse their spores. But it appears that this is not always the case. Lewis *et al.* (2014) considered the long-distance dispersal that was evidenced in *Tetraplodon* (Figure 55, Figure 58-Figure 59). The amphitropical disjunctions required explanation. The researchers compared stepwise migration along the Andes, direct long-distance dispersal, and ancient vicariance. Using four loci from each of 124 populations throughout the global range, they analyzed genetic evidence for the dispersal pathway. Three clades emerged, indicating three pathways of dispersal. There is no evidence of modern or historical wind connectivity between the polar regions, and these spores are not easily dispersed by wind. The researchers concluded that migratory birds most likely accounted for the long-distance dispersal of *Tetraplodon*, suggesting that the order Charadriiformes were the most likely dispersers.

Additional information on birds that eat capsules is in Volume 2, Chapter 16-2.

Mammals

Both large and small mammals step on bryophytes. Fur and hooves are likely to carry at least some forms of bryophyte propagules. Pauliuk *et al.* (2011) investigated dry grassland dispersal by sheep. They collected gametophyte fragments from the fleeces and hooves of 12 sheep, including two breeds. They also grew microscopic diaspores collected from soil that adhered to the hooves. Among the species in the pasture, 40% were transported, comprising 16 moss species. Sheep breeds collected different arrays of species, with dense, curly fleece carrying more fragments and larger species than sheep with smooth and fine hair. Pleurocarpous species, small species, and mats were represented more frequently in proportion relative to the vegetation; large species, acrocarpous life forms, wefts, and turfs were underrepresented. Hooves carried mostly acrocarpous colonist species.

In the Arctic, *Voitia hyperborea* (sometimes considered a variety of *V. nivalis*; Figure 25) has a capsule that does not open (Steere 1974). It appears that musk oxen and caribou may help in dispersal by chewing on the capsules as they graze other plants. In any event, it would seem that some animal agent is necessary for the dissemination of spores. During (personal communication, 29 May 2006) suggested that whole capsules may possibly be dispersed, but that the spores in *Voitia nivalis*, at least, have a structure that suggests they are sticky like those of other genera of the **Splachnaceae** and may adhere to beetles or even larger animals once the capsule begins to decay and expose them. More detail on the dung mosses is in the habitat subchapter on dung mosses.

In the Alps, *Voitia nivalis* is apparently dispersed by ruminants. It can be found in shelters or on the trails of sheep, chamois, and ibex, often on dry cliff ledges (Geissler 1982). This dispersal could carry fragments and other diaspores trapped on the feet and among fur or through feces holding spores inadvertently eaten along with forage.

There is some evidence that rodents contribute to the dispersal of fungal spores through ingestion and subsequent deposit of feces (Trappe & Maser 1976; Cázares & Trappe 1994; Janos *et al.* 1995). It is likely that rodents likewise contribute to bryophyte spore dispersal, not only through ingestion, but also by transporting spores in their fur. Others are likely to hitch a ride in mud on the feet. Nevertheless, it appears that direct data to support this role are lacking for bryophytes. We do know that rodents eat bryophytes, as shown for this mouse dining on *Funaria hygrometrica* capsules (Figure 109). Andrew Spink photographed a vole eating mosses (Figure 110).



Figure 109. Mouse eating *Funaria hygrometrica* capsules on Isle Royale, Michigan, USA. Photo courtesy of Steve Juntikka.

Matt Dami (Bryonet 26 August 2016) reported providing mice with capsules of the mosses *Dicranum flagellare* (Figure 111) and *Polytrichum commune*. They consumed the capsules and the fecal samples were collected and cultured on nutrient agar. Both species grew from the ingested spores, but *P. commune* (Figure 112) had much more germination success and far more vigorous growth.



Figure 110. Bank vole eating mosses in The Netherlands. Such close contact is likely to carry spores from the capsules seen in the picture. Photo by Andrew Spink, with permission.



Figure 111. *Dicranum flagellare*, a species whose spores survive the digestive tract of a moss. Photo by Bob Klips, with permission.



Figure 112. *Polytrichum commune* with capsules. Their spores seem to thrive when passed through the digestive tract of a mouse. Photo by Bob Klips, with permission.

Spores adapted for animal dispersal are sticky and elliptical, as in *Splachnaceae* (dung mosses) or *Schistostega pennata* (luminous moss), these being dispersed by flies. Beetles, earthworms, and slugs are likely dispersers, albeit for short distances. Ducks are known to carry spores, and small nesting birds may use setae and capsules in nests, but the effectiveness of these dispersal agents is unknown.

Water Dispersal

Conrad (1996) examined water samples in a *Taxodium* (bald cypress) swamp biweekly for spores. He also cultured both herbarium specimens and propagules from the diaspore bank. Although two other liverwort species regenerated from soil diaspores, *Ricciocarpus natans* (Figure 113) grew only from the spores (Figure 114) in the water samples and Conrad concluded that its presence in the swamps is entirely due to water dispersal.



Figure 113. Floating thalli of *Ricciocarpus natans*. Photo by Janice Glime.

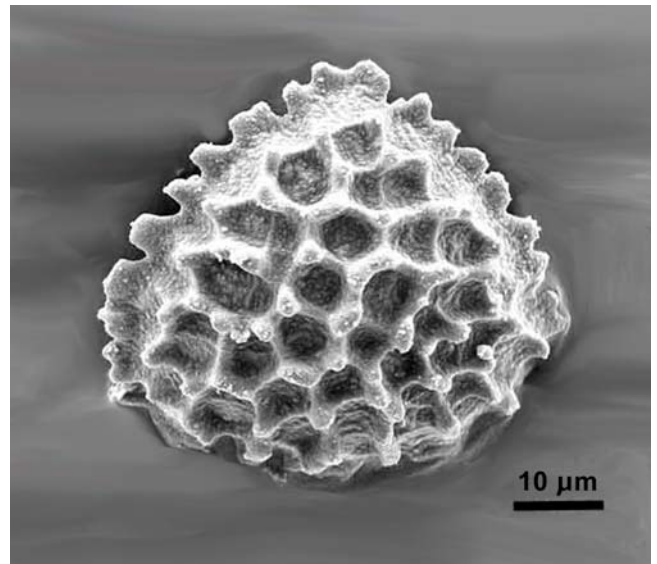


Figure 114. SEM of *Ricciocarpus natans* spore, a spore most likely transported by water. Depressions in the surface may aid in flotation. Photo by William T. Doyle, with permission.

Aquatic liverworts often have spines on their spores. Porsild (1903) believed that these served as attachment aids for spore dispersal by aquatic animals. However, other scientists believe that they instead act as anchors to hold

the spores onto rough surfaces so that not all are lost during heavy flows of streams (Studhalter 1933). In any case, some aquatic species, e.g. *Ricciocarpos natans* (Figure 114) and *Riccia fluitans* (Figure 115), do not have these spines, suggesting that the surface configuration may have more to do with phylogeny than with environment. On the other hand, they may aid flotation, permitting the water to carry them off.

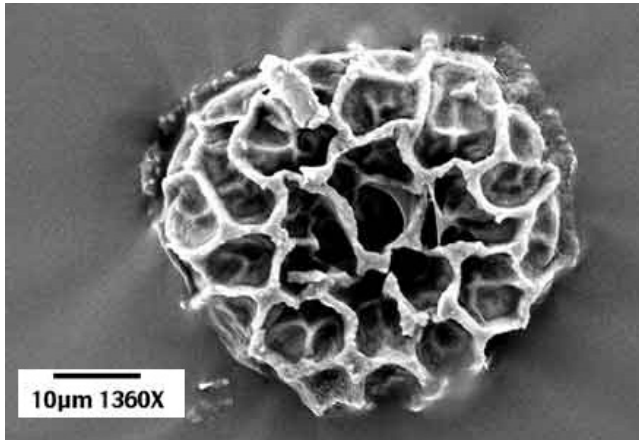


Figure 115. *Riccia fluitans* spore distal view SEM. Photo by William T. Doyle, with permission.

It is fairly common for rock-dwelling bryophytes of streams and rivers to project their sporophytes above the water level where they can be wind dispersed (Figure 116). This requires timing to produce sporophytes at a time when the water level is down.



Figure 116. *Hygrohypnum alpinum* with emergent capsules. Photo by Michael Lüth, with permission.

Common Adaptations

Mahabalé (1968) reviewed the characteristics of spores of aquatic tracheophytes. He found that the spores are short-lived and germinate quickly. These are water-dispersed. Those that are semi-aquatic or are facultatively aquatic have spores with thick outer walls and are dispersed by either insects or wind.

Cox (1983) tested the hypothesis that aquatic spores would have large, long axes and move in planes such as the

water surface, rather than in three dimensions. He also predicted a greater incidence of dioicism. He found that data supported these hypotheses for a variety of aquatic spores, including bryophytes. He also found that many spores had flotation devices. Cox considered these traits to provide "an efficient search vehicle." He considered dispersal in the aquatic environment to be a random search and that movement in one plane reduced that search territory.

As Mahabalé suggested, spores of the liverwort *Riccia gougetiana* (Figure 117) are over 200 μm in diameter (Schuster 1966); those of *Riella* (Figure 78) are 70 μm, nearly four times as large as the diameters of most air-dispersed spores (Mahabalé 1968; Cox 1983). *Pellia epiphylla* (Figure 118-Figure 119), a common streamside species, disperses its spores as a single mass (Cox 1983), but it also has elongate spores (Figure 119). *Gymnocolea* (Figure 120) uses deciduous perianths as its floating dispersal unit. Elongate dispersal units are seen in vegetative dispersal units such as fragments of *Fontinalis* (Figure 121) (Glime *et al.* 1979).



Figure 117. *Riccia gougetiana*, a species with 200 μm spores. Photo by Jonathan Sleath, BBS website, with permission.



Figure 118. *Pellia epiphylla* capsule dehiscent, showing clumps of spores. Photo by Ralf Wagner at <www.dr-ralf-wagner.de>, with permission.



Figure 119. *Pellia epiphylla* spore. Photo by Ralf Wagner at <www.dr-ralf-wagner.de>, with permission.

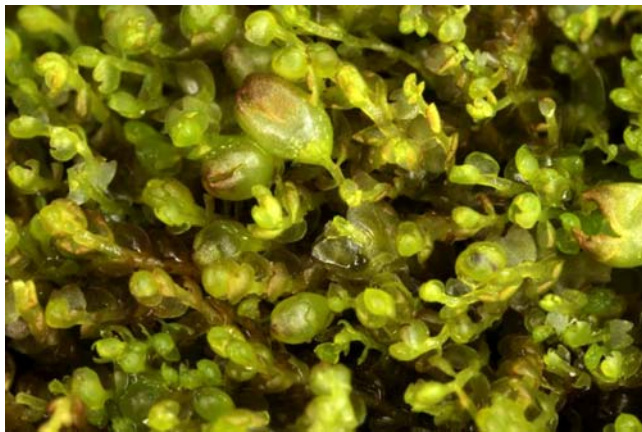


Figure 120. *Gymnocolea inflata* showing enlarged, oblong terminal perianths. Photo by Jan-Peter Frahm, with permission.



Figure 121. *Fontinalis dalecarlica* fragments imbedded in ice from a stream in New Hampshire, USA. Photo by Janice Glime.

Marine Dispersal?

No species is known to grow in marine waters, but Engel and Schuster (1973) raised the question of marine dispersal. They reasoned that species subject to tidal action or ocean spray were the best candidates. They assumed that bryophytes would not survive long exposures to salt water and presumed that freshwater drainage from adjacent forests above the beach and high rainfall made it possible

for species subjected to saltwater to survive. Hence, they concluded that marine dispersal was not possible, but this has not been tested.

Flood Plains and Dry Flats

Volk (1984) suggested that the distribution of spores by animals is most important for genera like *Riccia* (Figure 117) that inhabit seasonally dry habitats, particularly in southwest Africa and the Mediterranean. Whereas annual species of *Marchantiales* produce large numbers of spores, in the perennial species spore number is typically reduced and is even more rare among species with bulbils. Those that do support significant spore production can have ornamented spores that facilitate transport by animals, or perhaps aid in flotation. Despite the periodic invasion by water, this may not be an effective means of dispersal to carry the spores to new locations. Large flooding episodes can bury spores and other propagules so much that they may not resurface for decades (Figure 122-Figure 123).



Figure 122. Eroded material transported by water to River Baihe, a tributary of Yellow River, Tibet. Photo by Sven Bjork, with permission.



Figure 123. Floodplain on Isle of Wight. This magnitude of flood is reached once in ten years. Photo through Wikipedia Creative Commons.

Schuster (1966) considered the dispersal of *Riccia* (Figure 124) and *Ricciocarpos* (Figure 114) spores by mud and water to be very frequent. They typically grow at the margins of rivers and streams in the floodplain, where their spores mature in spring or in late summer or fall when flooding is common. The hornwort genus *Notothylas* (Figure 125) is also likely to be dispersed in this way. In *Riccia* (Figure 124) and *Sphaerocarpos* (Figure 126), the

spores are exceptionally large (65-200 μm diameter), are accompanied by elaters, and are dispersed by water.

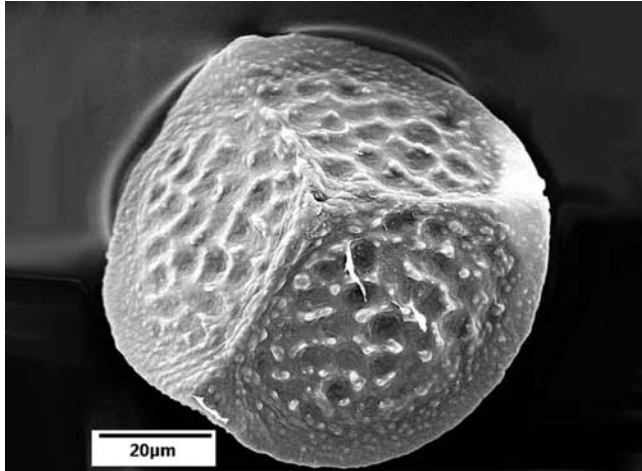


Figure 124. *Riccia beyrichiana* spore proximal view SEM, showing its larger size compared to that of *Notothylas*. Photo by William T. Doyle, with permission.

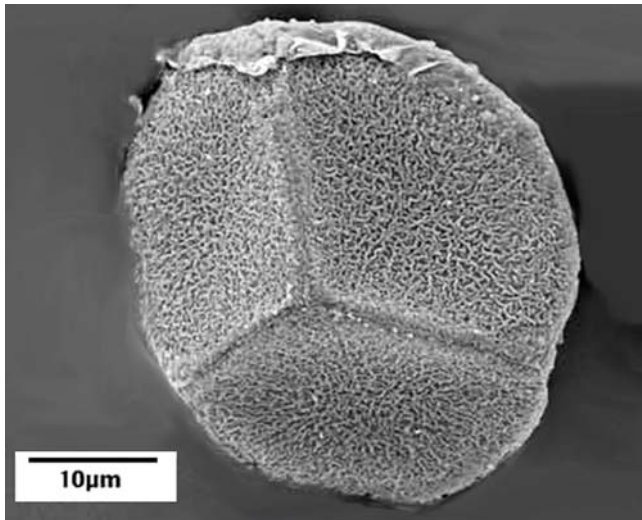


Figure 125. *Notothylas obicularis* spore proximal view SEM. Photo by William T. Doyle, with permission.

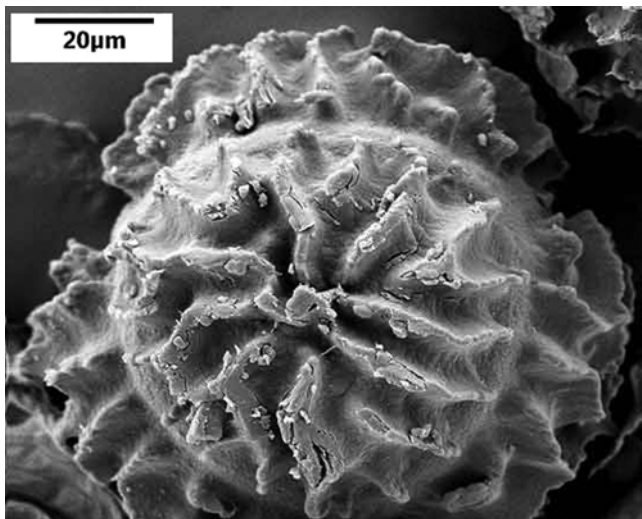


Figure 126. *Sphaerocarpos stipitatus* distal spore wall SEM. Photo by William T. Doyle, with permission.

Raindrops

The genus *Diphyscium* (Figure 127) has a flat side on its capsule. Crum (1983) reports that raindrops hitting this flat side can cause "little puffs" of spores that are propelled up to 5 cm from the capsule. It could be that the same phenomenon occurs in *Buxbaumia*.



Figure 127. *Diphyscium foliosum* flat-topped capsules where raindrops expel spores. Photo by Hermann Schachner, through Creative Commons.

Exploding Capsules?

Lacking peristome teeth, *Sphagnum* has an explosive capsule that behaves much like an air gun. It exerts an internal pressure of 4-6 atmospheres, a pressure equal to that of the "huge tires of heavy trucks" (Crum 1973). If you place mature capsules under a lamp with a tin cup or other "roof" to catch the spores, you can hear the capsules pop as the lids strike the cover, a phenomenon reported by one of the bryologists following a *Sphagnum* collecting trip at a *Sphagnum* conference in Great Britain. Some bryologists claim to have heard the capsules popping in the field, with the sound being generated entirely by the explosions of the capsules.

Vortex Rings

This explosion is a necessary event for the toothless *Sphagnum* to get its spores above the **laminar flow** region near the capsule and into the **turbulent flow** that can carry the spores away from their parent. But it seems that this is more than just a straight shot. Whitaker and Edwards (2010) report what seems to be the first evidence of plants using a **vortex ring** (Figure 128-Figure 129). The vortex ring is a self-sustaining flow field that can carry one fluid (in this case, a mass of spores) through another (in this case, the surrounding atmosphere) without significant drag. The result is that spores go farther.

When the spores explode from a *Sphagnum* capsule, this vortex ring, shaped like a mushroom cloud, forms and dissipates very quickly above the capsule (Figure 129). As the spores are ejected from the capsule, they are "entrained by the co-moving vortex bubble that forms at the lip of the capsule and moves upward" (Figure 130). The advantage of this vortex ring is that it moves the spores much farther than an air-gun mechanism could. This is the result of a self-sustaining flow field that moves the donut-shaped mass of spores upward.

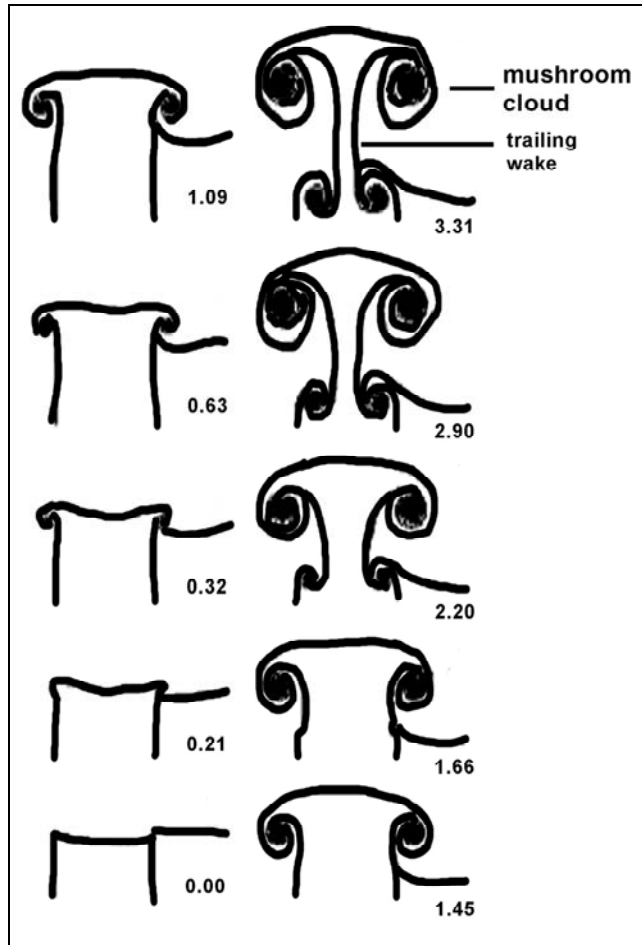


Figure 128. The development of a vortex ring with its mushroom cloud and trailing wake following the expulsion of a *Sphagnum* operculum. Redrawn from Whitaker and Edwards at <www.math.lsa.umich.edu>.



Figure 129. *Sphagnum* spore vortex taken as a time series every 100 microseconds. Photo by Clara Hard, Joan Edwards, and Dwight Whitaker from Whitaker & Edwards 2010, with permission.

The large number of spores (~100,000) in a single capsule form a bubble with a radius of 5 mm (Whitaker & Edwards 2010). These vortex rings cause a thrust augmentation by acceleration of the additional ambient fluid created at the time of the explosion (Krueger *et al.* 2008). The ring itself is "generated by the transient ejection of a jet from a tube or orifice" such as the opening of the *Sphagnum* capsule.

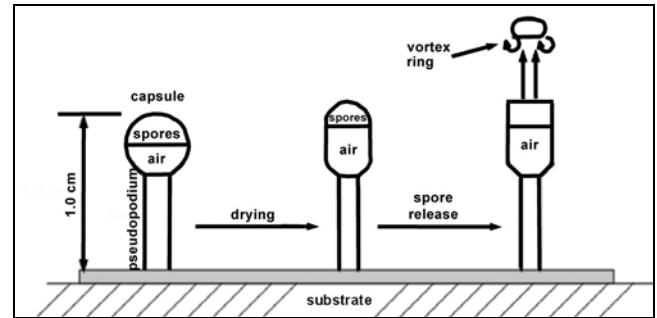


Figure 130. *Sphagnum* spore capsule from fresh to drying to release of the operculum. Redrawn from Miller 2010.

As Mustain (2010) points out, it is these vortex rings that help the squid speed through the water and the human heart to push blood from chamber to chamber. They are present in the clouds arising from an erupting volcano and propel jellyfish in the sea (Krueger *et al.* 2008). For *Sphagnum*, it permits this short plant to place its spores (Figure 131) into the winds that start about 10 cm above the surface (Whitaker & Edwards 2010). The ring keeps the spores together, preventing their useless descent to the ground. They calculated that the vortex ring typically shoots more than 11 cm into the air, sometimes as high as 17 cm. Furthermore, Johan L. van Leeuwen from the Netherlands' Wageningen University (in Mustain 2010) reports that this shot of spores reaches about 144 kph!

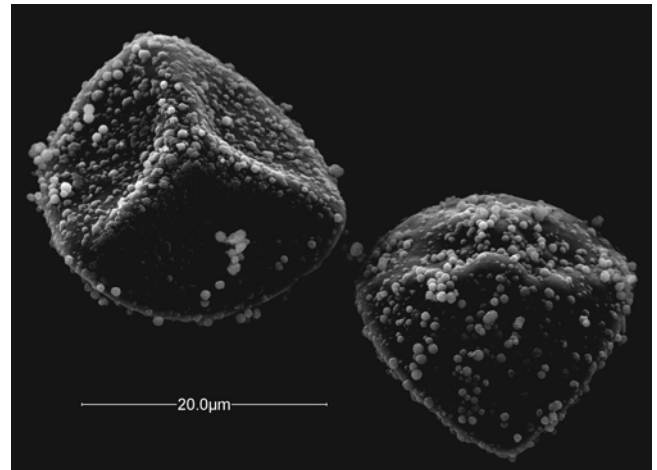


Figure 131. *Sphagnum* spores SEM. Photo by Dwight Whitaker and Joan Edwards, with permission.

Role of Stomata

Unlike many of the other bryophytes, *Sphagnum* has its stomata located away from the base and top of the capsule, suggesting that their function might be different. Boudier (1988) reported that the stomata of *Sphagnum* were not, as assumed, involved in any respiratory function in this genus, but rather that they are "false stomata" that give the capsule hardness and give the capsule wall flexibility. Beerling and Franks (2009) added to this that they were of importance in controlling and facilitating water loss from the capsule. Chater *et al.* (2011) determined that the stomata of bryophytes, like those of tracheophytes, are under the control of ABA and respond to environmental signals in the same way as guard cells of

tracheophytes. Duckett *et al.* (2009, 2010a) conducted further experiments by pricking the *Sphagnum* capsules and demonstrating that both intact and pricked capsules dried out and dehisced over an 8-12 hour period. During this time the stomatal guard cells gradually collapsed. This seems to be in direct contradiction to the assertion of Ingold (1959), who concluded that the dehiscence mechanism of *Sphagnum* capsules depends on a capsule wall that is impermeable to gases. Ingold suggested that cuticularization of the guard cells with age could block the air passage. Duckett *et al.* (2009, 2010a) contend that, rather than an air-gun explosion (as understood by Ingold), the spore discharge results when differential shrinkage of the capsule walls causes the rigid operculum to pop off.

The shrinkage of the *Sphagnum* capsule wall has been known for some time. Maier (1974) described the importance of a rigid zone of resistance in the capsule wall that permits the capsule to maintain its diameter even as the remainder of the capsule shrivels as it dries. This rigid wall tissue causes the shape of the capsule to change from spherical to cylindrical. This causes maximum stress in the area of the operculum, causing the wall (line of dehiscence) to break.

Duckett *et al.* (2009, 2010a) concluded, as did Boudier (1988), that the only role for the stomata in *Sphagnum* is to aid in capsule drying and thus shrinkage. Duckett *et al.* determined that there is no potassium-regulating mechanism for these guard cells.

The behavior of guard cells in *Anthocerotophyta* (Figure 133-Figure 136) seems to be support for the dispersal role. Lucas and Renzaglia (2002) found that the guard cells in this group do not respond to abscisic acid (ABA). Furthermore, in young tissues K^+ and malate are localized in all epidermal cells, but once the tissues mature, they occur only in the guard cells. This permits them to serve as an osmoticum that causes the guard cells to swell due to water influx. This behavior is coupled with a pattern of function in which the guard cells do not respond to light (Lucas & Renzaglia 2002; Duckett *et al.* 2010b). Rather, they begin closed in young tissues, then open as tissues mature, and remain open. This behavior permits older epidermal tissues to dry out (Figure 136). Duckett *et al.* (2010b) suggest that the same mechanism is at work in mosses. Such drying could contribute to dispersal.



Figure 132. *Anthoceros agrestis*, showing involucre where stomata are young and closed and capsule where stomata are mostly mature and open. Photo by Jan-Peter Frahm, with permission.

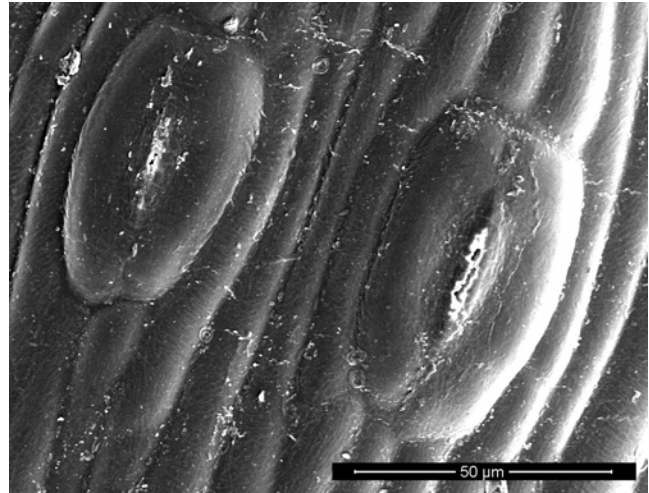


Figure 133. SEM of *Anthoceros punctatus* stomata in the sporophyte. Photo courtesy of Jeff Duckett and Silvia Pressel.

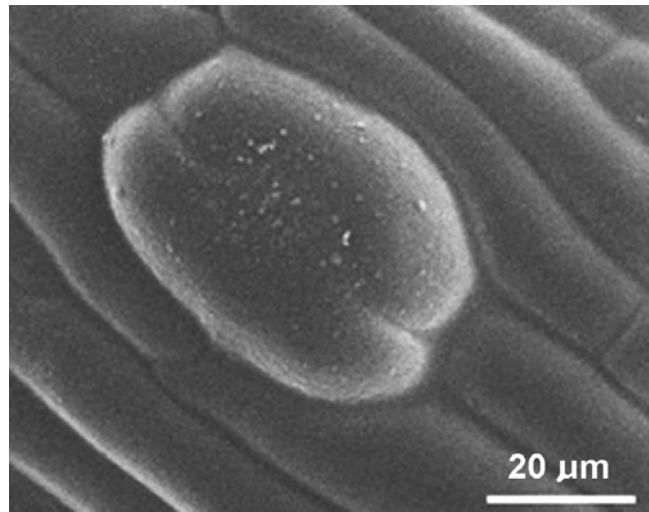


Figure 134. *Paraphymatoceros minutus* closed stoma from inside involucre. Photo modified from Jeffrey Duckett, Ken P'ng, Karen Renzaglia, and Silvia Pressel, with permission.

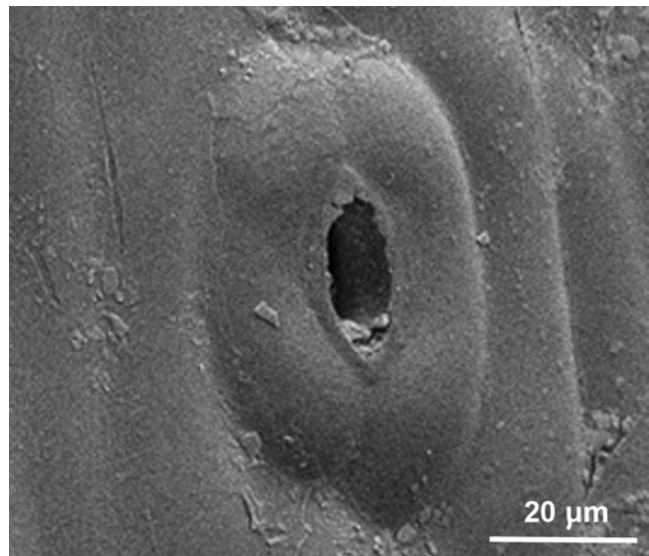


Figure 135. *Paraphymatoceros minutus* newly opened stoma from immediately above involucre, *i.e.* older tissue than that within the involucre. Photo modified from Jeffrey Duckett, Ken P'ng, Karen Renzaglia, and Silvia Pressel, with permission.

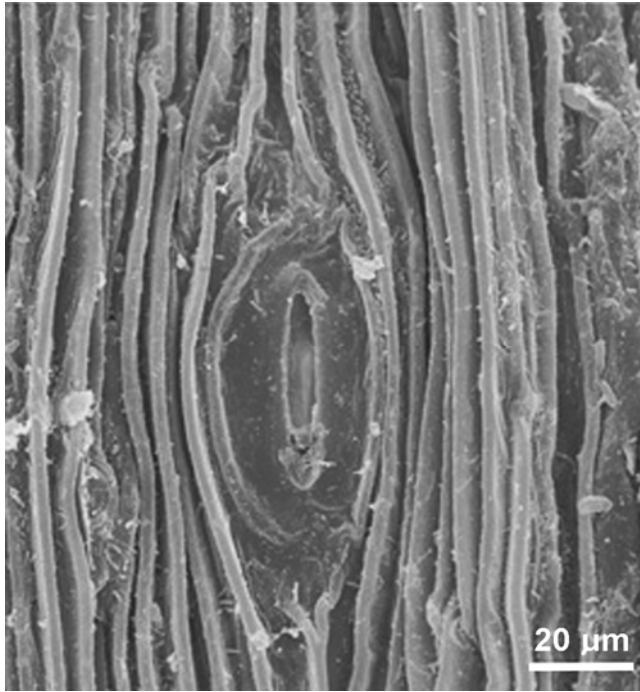


Figure 136. *Phaeoceros laevis*, open stoma flanked by desiccated and shrunken epidermal cells well above dehiscence point. Photo modified from Jeffrey Duckett, Ken P'ng, Karen Renzaglia, and Silvia Pressel, with permission.

The functioning of bryophyte guard cells has been largely ignored. Pressel *et al.* (2014) followed their development in hornworts and determined that the guard cells contain giant, starch-filled chloroplasts as they begin to differentiate. These chloroplasts divide, regaining their spherical shape after the aperture opens. After opening of the guard cells, wall material accumulates over them and wax rodlets line the pores. Pressel and coworkers considered it unlikely that the guard cells moved after maturity, based on the widespread presence of open guard cells. This propensity to remain open suggests that the stomata may function in facilitating the desiccation of the sporophyte, ultimately facilitating dehiscence and dispersal.

If guard cells do indeed function to facilitate dispersal by drying the capsule, then those species with few guard cells should have diminished dispersal capacity. Sundberg (2010a) cites some species within the *Sphagnum* section *Subsecunda*, including *Sphagnum cyclophyllum* (Figure 137), *S. microphyllum*, *S. macrophyllum* (Figure 138), and *S. pylaesii* (Figure 139), as species that have small, thin-walled capsules with short pseudopodia, large opercula, and no or few pseudostomata. Hence, they have no explosive discharge of spores (Andrews 1960, 1961; Shaw *et al.* 2004). These same species have only limited geographic distribution, suggesting that the lack of stomata and explosive discharge may contribute to a limited dispersal. On the other hand, Sundberg (2010a) found that 14 boreal species with circumpolar or amphi-Atlantic distributions, including four species with a distribution also in the southern Hemisphere, (Daniels & Eddy 1990) have the explosive dispersal mechanism.



Figure 137. *Sphagnum cyclophyllum*, a species that lacks explosive discharge of spores. Photo by Blanka Shaw, with permission.



Figure 138. *Sphagnum macrophyllum*, a species that lacks explosive discharge of spores. Photo by Janice Glime.



Figure 139. *Sphagnum pylaesii*, a species that lacks explosive dispersal of spores. Photo by Michael Lüth, with permission.

But what about the role of stomata in other bryophytes? Only *Sphagnum* has the reputation of an explosive discharge. Stomatal density in non-*Sphagnum* mosses can depend on the environment, at least in some members of the *Polytrichaceae* (Figure 140-Figure 141). Szymanska (1931) found that even within the same species,

plants in moist habitats had more stomata per mm². This supports the concept that the stomata are used to help dry the capsules, although not necessarily resulting in any "explosion." Abella *et al.* (1999) found no taxonomical value for the stomata in ten species of **Pottiaceae**, so perhaps these numbers too respond to the environmental humidity or differ with habitat dryness among species within a genus.

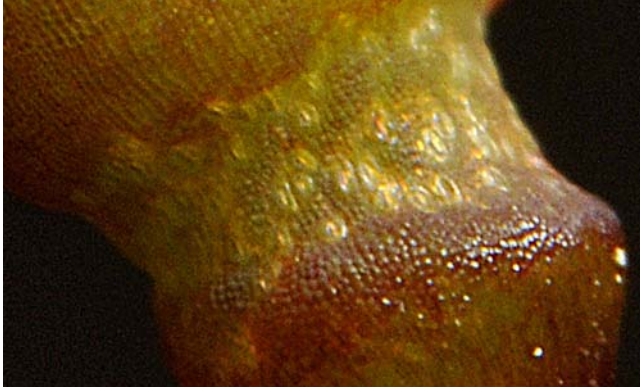


Figure 140. *Polytrichum* sp. stomata on capsule. Photo by George Shepherd, through Creative Commons.

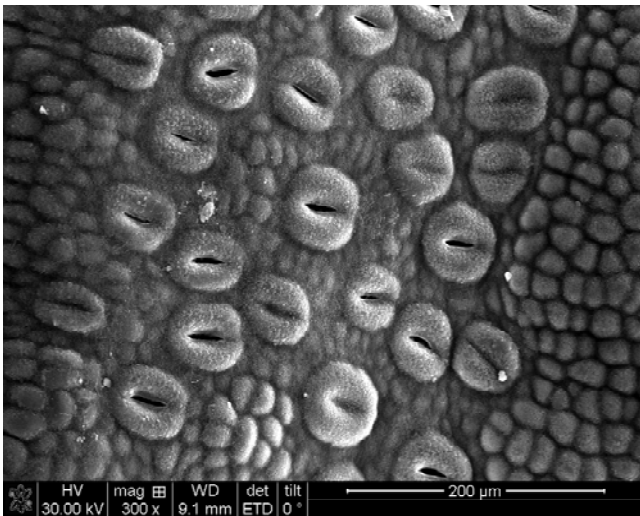


Figure 141. Stomata on neck of *Polytrichum juniperinum* capsule. Photo courtesy of Jeff Duckett and Silvia Pressel.

Egunyumi (1982) found correlations between stomata number and seta length in tropical African mosses, represented by 29 species in 12 families. These stomata ranged in number from 2 to more than 200 per capsule. This relationship might also reflect humidity of the habitat, but more data are needed to support this idea. Egunyumi found that stoma size correlated significantly with epidermal cell size, a taxonomic character. Stomatal position differed among species, with *Wijkia trichocoleoides*, *Trichosteleum microcalyx*, *Stereophyllum radiculosum* (Figure 142), and *Stereophyllum virens* having stomata raised above the level of epidermis, whereas in *Brachymenium leptophyllum* and *Bryum coronatum* (Figure 143) they were sunken.

In their work on *Funaria hygrometrica* (Figure 144), Sack and Paolillo (1983) found that subsidiary cells in that species actually have thickened walls close to the guard cell at maturity. They reported that the guard cell walls have

thin areas that are capable of flexing. The guard cell also has fibrillar layers that are oriented both axially and radially with respect to the pore. It seems that few guard cells in bryophytes have been described in such detail, but the structure is sounding a lot like that of tracheophyte guard cells. The role of stomata in spore release seems to be a promising area for research.



Figure 142. *Stereophyllum radiculosum*, a moss that has its stomata raised above the capsule epidermis. Photo by Niels Klazenga, with permission.



Figure 143. *Bryum coronatum* with capsules that have sunken stomata. Photo by Jan-Peter Frahm, with permission.

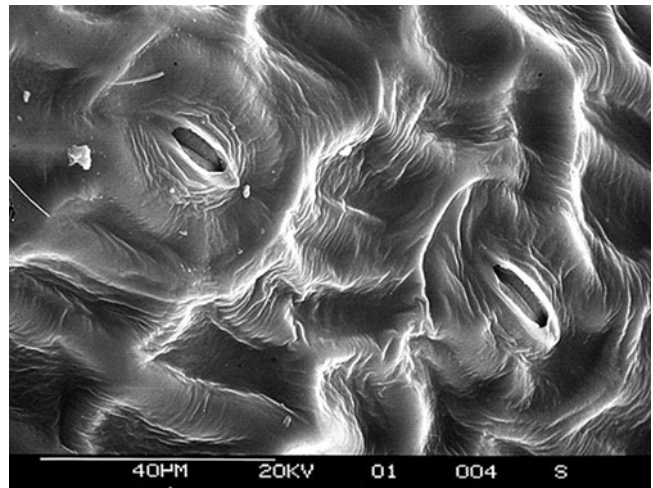


Figure 144. *Funaria hygrometrica* stomata. Photo from Botany 321 Website, UBC, with permission.

Is This an Explosion in *Sphagnum*?

Here we may have a semantic problem, with Duckett *et al.* (2009, 2010a) attempting to dispel our long-held interpretation of the method of spore expulsion by declaring it "not an air gun." But is it an explosion? While explosion can be defined as "a release of mechanical, chemical, or nuclear energy in a sudden and often violent manner with the generation of high temperature and usually with the release of gases" – certainly not descriptive of this event – the term has gained much broader meanings. Among these, we might be more comfortable with "a violent blowing apart or bursting caused by energy released from a very fast chemical reaction, a nuclear reaction, or the escape of gases under pressure." The question to be resolved is whether there are gases under pressure. Whereas Duckett *et al.* have demonstrated that the operculum is released by the distortion of the capsule, an internal pressure is necessary to qualify this as an explosion. If indeed Crum (1973) is right and the internal pressure is 4-6 atmospheres, then the release of this pressure upon dehiscence of the capsule fits at least one definition of an explosion. In any case, a vortex ring results, and that seems to be visual proof that pressure has been released.

Sundberg (2010b) disagrees with the interpretation of Duckett *et al.* (2009, 2010a) and contends that it truly is an air-gun ejection of spores. He points out that approximately 35% of the *Sphagnum* capsule volume is air. To test the role of the stomata in producing this gun, Sundberg used *S. centrale* (Figure 145) and *S. fuscum* (Figure 146). Using 16 capsules of each species, he pricked half of them in the lower half into the interior (ca 1 mm deep). Within 12 hours, all but one of the capsules had dehisced, with the ones not pricked presenting audible snaps. Spores from not-pricked capsules were ejected 50-150 mm, leaving the capsules nearly empty. The pricked capsules, on the other hand, also opened their lids, but no snap could be heard and the spores only spilled in clumps in a heap below the capsule opening, discharging only 5 mm or less. He considered this evidence that the normal discharge was explosive.



Figure 145. *Sphagnum centrale*, a species that disperses its spores explosively. Photo by Janice Glime.



Figure 146. *Sphagnum fuscum* with capsules, a species that ejects its spores explosively. Photo by Dale Vitt, with permissions.

Falling Rate

Using a filming technique similar to that of Whitaker and Edwards (2010), Sundberg (2010a) examined the settling speed of spores from 14 species of *Sphagnum*. They determined a maximum discharge speed of 3.6 m s^{-1} and a maximum height of 20 cm (mean 15 cm). The cloud (vortex ring) size was positively related to capsule size, giving species with larger capsules a dispersal advantage. Half the spores remained in clumps, usually of 2-4 spores. Single spores, with a deltoid shape, settled at $0.84\text{-}1.86 \text{ cm s}^{-1}$, a speed about 52% slower than would be expected for spherical spores of the same diameter. Larger spores settled faster, following Stokes' law. Sundberg suggested that the combination of the added height from the explosion and the slow settling speed serve to increase dispersal distance and may account for the wide distribution of boreal *Sphagnum* species. On the other hand, Fenton and Bergeron (2006) suggested that *Sphagnum* invasion into young dense forests might be dispersal limited, but they allowed for the possibility of unsuitable available substrata. It is likely also that the forest interfered with dispersal, trapping spores on bark and among the leaves.

A *Sphagnum* Spore Mimic

This spore dispersal mechanism is so good that it has been stolen by the fungus *Bryophytomyces sphagni* (Ascomycota) (Currah & Davey 2006). This parasite grows in the capsules of *Sphagnum*, replacing the *Sphagnum* spores with its own. This does nothing to interfere with the capsule explosion. Hence, the fungal spores are dispersed in that same manner as would have been for the *Sphagnum* spores.

Summary

Spores are the most successful agents of long-distance dispersal in bryophytes, whereas vegetative means help the population to become established and spread once having arrived. **Peristome teeth** in mosses, an **explosive capsule** in *Sphagnum*, and **elaters** in liverworts help in dislodging spores and dispersing them. Most bryophytes are adapted for wind dispersal, with the occasional updraft or gust permitting somewhat greater distances. However, the majority of

spores seem to land within 2 m of their parents. Invasive species seem to benefit from both rapid vegetative dispersal and long-distance travel.

Cleistogamous capsules require capsule decay for dispersal, relying on distribution by animals, especially invertebrates, or becoming established near home. Capsules of taxa like *Buxbaumia*, on the other hand, often split despite having teeth and may rely on such insects as fungal gnats to disperse spores.

Earthworms can transport spores on their moist surfaces or through the gut, and theme may be transported further if the earthworms are eaten while carrying the spores.

Animal dispersal in **Splachnaceae** and *Schistostega pennata* is facilitated by sticky, elliptical spores, and in the case of **Splachnaceae**, also by odors. Other animal dispersal appears to be chancier, with ducks, beetles, ants, slugs, earthworms, and small nesting birds contributing.

Water dispersal is important for water-dwelling species, and in floodplain taxa, a dormancy mechanism is usually necessary. Dormancy also provides spores with the ability to survive in the soil below 1 cm where they do not receive light and therefore will usually not germinate in the presence of water. Dispersal may be facilitated by decorations on the spores that create air pockets, aiding flotation. Others have spines and hooks that may aid in animal attachment and dispersal.

Raindrops on the flat side of a *Diphyscium* capsule help to discharge the spores.

Stomata seem to play a role in dispersal by facilitating drying of the capsule. In *Sphagnum*, the ejection of spores is explosive, forming a **vortex ring** that drives the spores about 10c m into the air, enough to get them into the air stream. This mechanism is so effective that the fungus *Bryophytomyces sphagni* lives in the *Sphagnum* capsule and is dispersed by the same mechanism.

Acknowledgments

I thank Joan Edwards for her patience in helping me to understand the vortex ring mechanism. Juan Carlos Villarreal sent me literature that was not available to me. Karen Renzaglia provided images that I requested for specific purposes. Jeff Duckett and Silvia Pressel permitted me to rummage through their images to find ones I needed to illustrate this chapter. Steve Trynoski offered several suggestions after a critical reading of this subchapter.

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CHAPTER 4-10

ADAPTIVE STRATEGIES: VEGETATIVE PROPAGULES

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CHAPTER 4-10

ADAPTIVE STRATEGIES: VEGETATIVE PROPAGULES



Figure 1. Deciduous branch tips of *Campylopus cryptopodioides*. Photo by Michael Lüth, with permission.

Vegetative Reproduction

Vegetative reproduction comes in many forms. These range from breakage of leaves and stems that have become brittle through desiccation to specialized gemmae that occur on leaves or special stems and are nurtured by the parent plant, ready to go when finding a suitable substrate, to tubers that occur on roots and protonemata.

Such asexual structures seem to have evolved through **heterochrony** (developmental change in the timing of events, leading to changes in size and shape), including **neoteny** (retention of juvenile characteristics in adults of species) (Newton & Mishler 1994). Hence, we can see gemmae that look like reduced leaves, as in *Aulacomnium* (Figure 2).

We might assume that in disturbed habitats, such as industrial areas, vegetative means to reproduce might offer advantages over more fragile-seeming protonemata necessitated by spore dispersal. But this is not always true. Nordhorn-Richter (1982) found the extent of bryophyte distribution in an industrial area of Germany was not improved by presence of asexual propagules except among members of *Plagiothecium* (Figure 3-Figure 4). On the other hand, vegetative reproduction offers the advantage of being ready to start developing an adult plant, reaching maturity much more quickly than a plant from a spore. Furthermore, bryophytes produce asexual propagules at a younger age than that needed for sexual reproduction.



Figure 2. *Aulacomnium palustre* gemmae that are modified leaves. Photo by Zen Iwatsuki, with permission.



Figure 3. *Plagiothecium laetum*. Photo by Christian Peters, with permission.



Figure 4. *Plagiothecium laetum* leaves with scattered gemmae. Photo by Kristian Peters, with permission.

Longton and Schuster (1983) listed six basic means of asexual reproduction in bryophytes:

1. multiple gametophores from the protonema of one spore

2. decay of older gametophyte parts with the separation of younger parts
3. development of multiple shoots by rhizomes and stolons
4. development of gametophores from rhizoids
5. regeneration from fragments
6. production of specialized "propagula."

Frey and Kürschner (2011) shortened and summarized this list, identifying three types of asexual reproduction that are recognized today:

1. asexual reproduction *s. str.* by **regeneration** from somewhat specialized caducous organs (leaves, leaf apices, shoots, branches, bulbils) and by production of specialized propagules (gemmae, protonemal brood cells, tubers)
2. **fragmentation** of plants or parts of plants into essentially unspecialized fragments
3. **clonal** reproduction (cloning from branches, stolons, and rhizomes).

Cloning results when a branch of a protonema or a plant becomes separated from its parent. This can occur by decay of the protonema or disintegration of plant modules. In gametophores, cloning requires the formation of **ramets** (individuals, "daughter plants"). Frey and Kürschner (2011) consider cloning to be a "keystone factor for asexual reproduction, habitat colonization, and habitat maintenance." While this cloning mechanism is not dispersal in the usual sense, it does contribute to placing the species in new locations. For example, when we (Zhang, Raeymaekers, and Glime, unpublished) mapped the locations of *Pleurozium schreberi* (Figure 5) in m² plots and followed them yearly for five years, we found that they appeared to "move" from one location to another within the plot, often changing position by several centimeters, sometimes forming two clumps.



Figure 5. *Pleurozium schreberi* in the boreal forest. Photo by Janice Glime.

Although sexual reproduction may provide the opportunity for new gene combinations, a number of bryophytes [e.g. *Cyrtomnium hymenophylloides* (Figure 6; Miller & Mogensen 1997)] persist without any evidence of sexual reproduction. In reviewing the literature, Rolstad & Gjerde (2003) considered that some bryophytes have poor dispersal capability due to the absence of spore production. In this case, vegetative diaspores and even fragments

maintain the species and carry it to new locations. As in *C. hymenophylloides*, the absence of sexual reproduction may only occur through part of its range, whereas other species seem never to produce capsules (Miller & Mogensen 1997). Rather, in *C. hymenophylloides* of North America and Greenland new growth arises from axillary and apical buds that appear to be the principal means of reproduction. Miller and Mogensen assumed that these were dispersed by wind but considered that water and gravity were also possible. It is interesting that populations may be all male, or more typically, all female.



Figure 6. *Cyrtomnium hymenophylloides*. Photo by Michael Lüth, with permission.

In general, not counting fragmentation, there seems to be only one type of asexual reproduction within a species (Li Zhang, Bryonet 16 March 2010). Nevertheless, many exceptions occur. Pressel *et al.* (2007) reviewed the propagules in *Bryum* (see below) and related genera. In this genus one can find rhizoidal and chloronemal tubers, axillary bulbils, chloronemal brood cells, and foliar and protonemal gemmae. *Ptychostomum* (= *Bryum*) *capillare* (Figure 7) and *Bryum dichotomum* (Figure 8) have three types, but only one type has been found in any individual at a given time (Imura 1994). However, Zhang found two types on the same individual of *Fissidens* sp. (Figure 9-Figure 12, Figure 112) – rhizoidal gemmae and tubers. Gemmae (Figure 10-Figure 12) in this species come in a variety of shapes and types. *Octoblepharum albidum* (Figure 13) has three modes (Zhang *et al.* 2003). In this species, new plants can grow from the leaf tips where first rhizoids are produced and then buds. These buds grow into plants and may, in turn, produce another "generation" of leaf-tip shoots, much like the walking fern *Asplenium rhizophyllum*. These walking mosses may constitute 5-20% of the population. *Leucobryum glaucum* (Figure 14-Figure 15; *Leucobryum* Figure 16) has a similar behavior in which the terminal rosette of leaves may produce rhizoids and new plants. But in this case, so far as is known, the new plants drop off and grow if they land on a suitable substrate.



Figure 7. *Ptychostomum* (= *Bryum*) *capillare* wet, a species that can produce caulonemal, rhizoidal, or leaf gemmae. Photo by David Holyoak, with permission.



Figure 8. *Bryum dichotomum*, a species with chloronemal, rhizoidal, and leaf gemmae. Photo by Michael Lüth, with permission.



Figure 9. *Fissidens taxifolius*. Photo by David Holyoak, with permission.



Figure 10. *Fissidens flaccidus* axillary gemmae on stem. Photo by Ida Bruggeman, with permission.



Figure 11. *Fissidens macaoensis* rhizoidal tuber. Photo by Li Zhang, with permission.

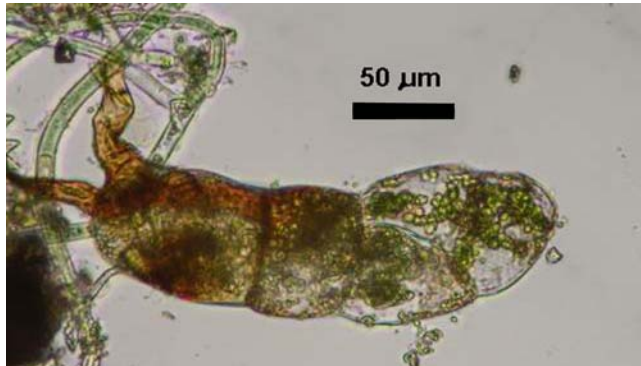


Figure 12. *Fissidens tenellus* bud. Photo by Tom Thekathyl, with permission.



Figure 13. *Octoblepharum albidum*, a moss that can grow new plants at its leaf tips, creating a walking fern type of reproductive strategy. Photo by Michael Lüth, with permission.



Figure 14. *Leucobryum glaucum* with young apical rhizoids. Photo by Nancy Ironsides, with permission.



Figure 15. *Leucobryum glaucum* with mature apical rhizoids that can serve as propagules. Photo by Sean Edwards, with permission.



Figure 16. *Leucobryum* showing rhizoids developing from leaf tips. Photo courtesy of Andi Cairns.

Pfeiffer *et al.* (2006) identified three types of vegetative morpho-types in the pleurocarpous moss *Rhytidium rugosum* (Figure 17): **ramet** (individual plant that has grown vegetatively from another individual, *i.e.*, a

branch, becoming part of a clone of that plant) that can become separated when they decay, brood **branch**, and **caducous** (easily detached) shoot apex. They demonstrated successful dispersal of vegetative diaspores through AFLP (amplified fragment length polymorphism) fingerprinting, wherein samples from one clone occurred on both studied plots in Germany. Furthermore, the close relationship of the fingerprinting between the two plots suggest clonal rather than sexual (spore) origin for the populations.



Figure 17. *Rhytidium rugosum* from Europe, showing what appear to be several ramets. Photo by Michael Lüth, with permission.

Dispersal of vegetative propagules seems to be more of a passive process than that of spores. Few special mechanisms are documented for removal of asexual propagules from the plant. *Tetraphis pellucida* (Figure 18-Figure 19), with apical gemmae in splash cups is a notable exception among mosses, with *Marchantia* (Figure 20-Figure 21) and *Lunularia* (Figure 22) species likewise having gemma splash cups. Others easily "pop" as they become detached by some intruder bumping them, as in *Dicranum flagellare* (Figure 23). The extent of transport by animals that brush against them has seldom been documented.



Figure 18. *Tetraphis pellucida* with gemma splash cups. Photo by Andrew Spink, with permission.

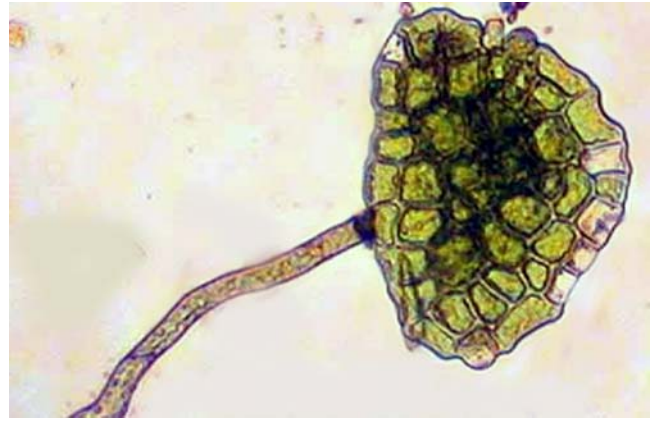


Figure 19. Gemma of *Tetraphis pellucida* showing protonema developing from it and lack of an apical cell. Photo from Botany website, UBC, with permission.



Figure 20. *Marchantia alpina* with gemma cups in Norway. Photo by Michael Lüth, with permission.

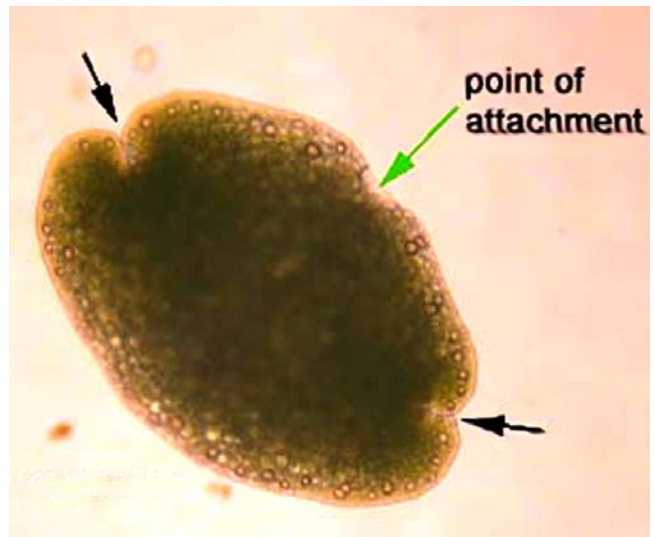


Figure 21. *Marchantia polymorpha* gemma showing notch (arrow) where growth begins. Photo by Kavita Uttam UBC, with permission.



Figure 22. *Lunularia cruciata* showing gemma splash cup. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.



Figure 23. *Dicranum flagellare* showing flagelliform branches that serve as propagules. It is accompanied by several species of the lichen *Cladonia*. Photo by Robert Klips, with permission.

Herben (1994) considers habitat to be the important parameter for assessing the role of the reproductive mode of bryophytes, with those in small and unstable habitats showing more frequent formation of propagules. Löbel and Rydin (2009) found that among epiphytes the habitat conditions had no influence on production of asexual propagules, whereas they did influence sporophyte production. Furthermore, sexual colonies had to reach a specific size before they could reproduce sexually, whereas there was no such limit for asexual reproduction. Despite the dispersal limitations of large asexual diaspores, asexual dispersal is still common among epiphytes, with higher growth rates for the asexual diaspores partially compensating for the limited dispersal. Furthermore, habitat turnover most likely favors asexual diaspores that start growth rapidly.

Löbel and Rydin (2009), working in the temperate zone, further considered that competition was not an important character in the epiphytic habitat because of the difficulty of dispersal and ability to spread vegetatively. Yu and Wilson (2001) pointed out the importance of patchiness and arrival times in plants, a concept that seems appropriate for bryophytes, especially epiphytes. They suggest that "trade-offs between different stages of colonization could be far more common in nature than a trade-off between competitive ability and colonization ability."

Botanists have traditionally considered vegetative reproduction (Figure 1) as making only limited contributions to genetic variability and new adaptation. But is this really the case, in particular, of bryophytes? Laaka-Lindberg *et al.* (2003) consider asexual propagules to have a significant role in bryophyte genetic dynamics.

In view of the vegetative propagation sources, Scrosati (2002) has offered a new definition of **genet** to allow for those plants such as bryophytes and algae that routinely propagate from vegetative cells: "For clonal autotrophic macroorganisms, in general, genet may be defined as a free-living individual that develops from one original zygote, parthenogenetic gamete, or spore and that produces ramets vegetatively during growth."

In bryophytes, only a few living cells may start a new plant. And it may be those very cells that are different, different in ways that endowed them, and them alone, to survive whatever killed the remainder of the plant. Through somatic mutations, individual cells may indeed be more adapted than the plant they occupy. And because of their small size, such fragments in bryophytes can be dispersed and serve as propagules. Each individual or part of an individual gametophore in the clone is capable of renewed growth upon relocation. However, while this scenario is theoretically possible, we have no clue how often it occurs.

While spores are the sexual means of reproduction and dispersal of mosses, providing a mechanism for recombination and variation, it is likely that most mosses rely more heavily on various vegetative means for their propagation (Anderson 1963; Steere 1965; Schuster 1966; Longton 1976, 1982; Selkirk 1984; Schofield 1985). For example, in three *Octoblepharum* (Figure 13) species in Panama, Korpelainen (1999) found that most populations consisted of a single genet, hence resulting from a single colonization event by one individual.

Clones can be very important in recolonization of minor disturbances. Frego (1996) reported on four boreal bryophytes and their ability to do so. *Pleurozium schreberi* (Figure 5) often has pure colonies in black spruce forest (*Picea mariana*). But it also has colonies with minor species as seeming invaders (Figure 24). Frego found that these minor species are able to persist by occupying small disturbance gaps in the *P. schreberi* colony. All of the species were able to colonize by encroachment of vegetative shoots. Propagules were important for this encroachment. *Pleurozium schreberi* was the most rapid colonizer, probably due to a combination of rapid growth and abundant vegetative propagules.



Figure 24. *Pleurozium schreberi* (center) and *Dicranum polysetum* (lower left), a common species combination in the boreal forest. Photo by Janice Glime.

Such reliance on asexual reproduction is due in part to the difficulty of completing sexual reproduction in many bryophytes. Since nearly 60% of the bryophytes are dioicous (Wyatt & Anderson 1984), and the monoicous habit usually provides more opportunity for sexual reproduction than the dioicous habit, it is easy to understand the importance of vegetative reproduction (Schofield 1985). Furthermore, some widely distributed species have never been found with sporophytes.

Dispersal potential is a major limiting factor on the distribution of bryophytes (Pohjamo *et al.* 2006). Hence, those species with mixed reproductive strategies have a greater chance of success. Pohjamo *et al.* suggest that such mixed strategies are particularly useful in a heterogeneous landscape where different means of reproduction have different levels of success in each of the microhabitats, and possibly in different years. Traditional thinking suggests that long distance dispersal is generally best by spores, whereas vegetative dispersal places the diaspores close to the parents, generally in the same environment. But what occurs when both are the same size?

Using trapping techniques, Pohjamo *et al.* (2006) tested this propagule size relationship for the leafy liverwort *Anastrophyllum hellerianum* (Figure 25-Figure 26), a dioicous inhabitant of **decorticated** (lacking bark) logs in their study area. This species produces gemmae on the branch apices, and these gemmae approximate the size of the spores. In their study, spore dispersal had little dependence on distance in the field or forest. The dispersal of gemmae was more strongly dependent on distance in the open than in forest sites. Rainy periods favored gemmae deposition compared to dry periods, perhaps due to effects of splashing. But weather seemed to have no effect on the dispersal pattern of either spores or gemmae. Gemmae provided the advantage of nearly continuous availability, whereas spore dispersal was seasonal. The striking revelation from this study is that gemmae, at least those of the same size as spores, can contribute to long-distance dispersal.

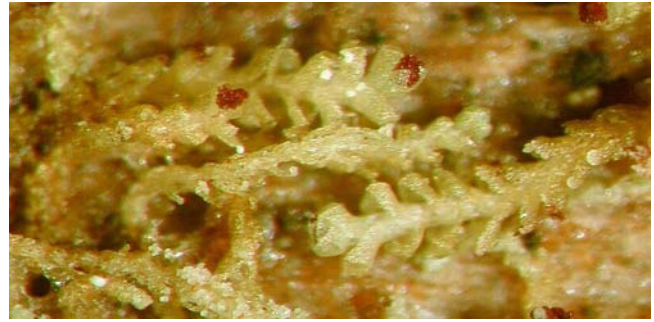


Figure 25. *Anastrophyllum hellerianum* with gemmae. Photo by Michael Lüth, with permission.



Figure 26. *Anastrophyllum hellerianum* gemmae. Photo by Des Callaghan, with permission.

Adaptations

There seems to be little information on adaptations of asexual propagules for dispersal or establishment. Thiers (1988) examined morphological adaptations of tropical rainforest **Jungermanniales**, including diaspores. She found that these diaspores had a secretion of sticky mucilage with discoid gemmae production. We can guess at some adaptations – projections that help bulbils adhere, dense starch storage in gemmae, thicker cuticles to reduce water loss, physiological ability to withstand desiccation, hormones (ABA) to induce dormancy, but these are guesses and remain to be tested as actual factors.

Fragmentation

Bryophytes have the ability to produce new plants from almost any part, making fragmentation a viable means of reproduction. Such a process requires that at least some cells lose their specificity (**dedifferentiate**), then differentiate into a new plant (Giles 1971). Giles considered that as long as cells remain on the parent plant, they will not dedifferentiate. But there are some indications among the leafy liverworts that such detachment is not always necessary before new plantlets are able to grow, particularly if the leaf is attached to a fragment rather than an attached plant (Fulford 1936; Glime 1970). This might suggest that the cells require a continuing source of an inhibitor to prevent dedifferentiation.

Fragmentation is the simplest form of asexual reproduction, a method used by the Japanese for the development of moss gardens (Ando 1971, 1987). Cells detached from virtually any part of a moss or liverwort are capable of regeneration into a new plant. This is true of leaves in which the tips dehisce to function as propagules (Reese 1997). Some of these devices are highly specialized, as for example, the caducous branchlets of *Leucodon andrewsianus* (Figure 27) where sporophytes are unknown (Reese & Anderson 1997).

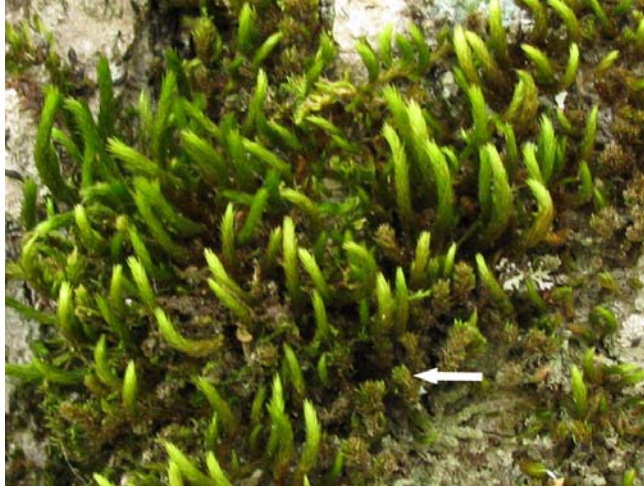


Figure 27. *Leucodon andrewsianus* on bark near Twin Lakes, Michigan. Arrow indicates caducous branchlets. Photo by Janice Glime.

Correns (1899) recognized the importance of the regenerative capacity of vegetative parts. They have historic importance in fossils as well. Miller (1985) reported fossil evidence that the dispersal and establishment of mosses had occurred as gametophyte fragments, suggesting that this is an ancient mechanism of reproduction and dispersal. This contention was supported by Lindskog and Eriksen (1995) who found fossil plant fragments in the debris layers of the ice core of a glacier in northern Scandinavia. These fragments compared well with the composition of the surrounding vegetation. Olga Belkina has supplied me with photographs indicating the presence of fragments and the establishment of colonies of *Hygrohypnella polaris* (Figure 28-Figure 30) on a glacier at Svalbard (Belkina & Mavlyudov 2011). Mosses are scattered across the glacier, as shown in Figure 31.

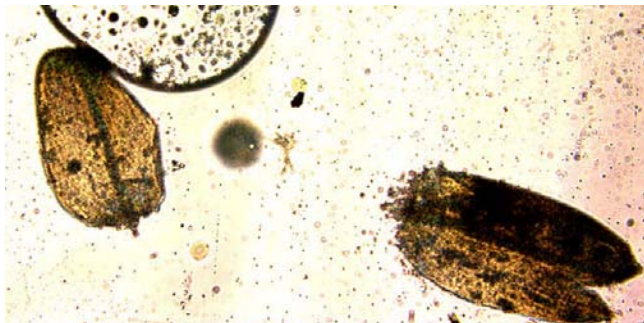


Figure 28. Fragments of *Hygrohypnella polaris* from glacier. Photo by Olga Belkina, with permission.



Figure 29. *Hygrohypnella polaris* on glacier. Photo by Olga Belkina, with permission.



Figure 30. Lower surface of *Hygrohypnella polaris* cushion with green branches and pedestal near it on glacier, indicating that it has been overturned and begun growth on the opposite side. Photo by Olga Belkina, with permission.



Figure 31. Austre Grøn fjordbreen glacier with the moss *Hygrohypnella polare* in the foreground. Photo by Bulat Mavlyudov, with permission.

Because vegetative reproduction tends to be more successful than that from spores, having fragments or specialized structures can be a safety net. For example, in experimental plantings of *Polytrichum juniperinum* (as P.

alpestre) (Figure 32), Miles and Longton (1990) could find no evidence that spores germinated in the field. However, new shoots formed readily from shoot fragments. In the same experiment, production of shoots from spores in the short-lived *Funaria hygrometrica* (Figure 33-Figure 34) was readily apparent. In *Atrichum undulatum* (Figure 43) and *Bryum argenteum* (Figure 35), many spores germinated, but often the gametophores failed to develop. Rather, those species, like the *Polytrichum juniperinum* (Figure 32), regenerated more easily from fragments.



Figure 32. *Polytrichum juniperinum* (= *P. alpestre*), a species that forms new shoots easily from apices. Photo by Des Callaghan, with permission.

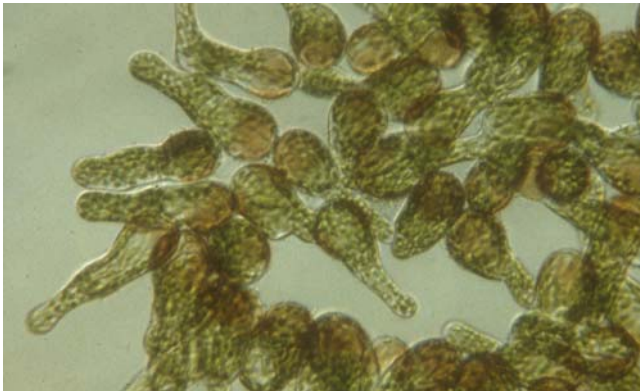


Figure 33. Germination of spores of *Funaria hygrometrica*. Photo by Janice Glime.

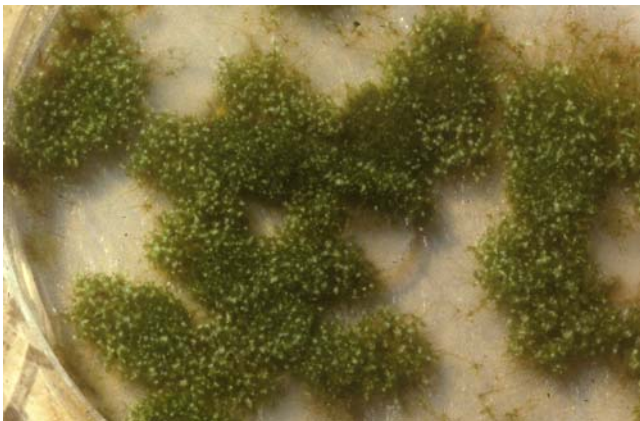


Figure 34. Young plants of *Funaria hygrometrica* germinated from spores. Each clump is the result of one spore, demonstrating the large number of vegetative reproduction by buds on the protonemata. Photo by Janice Glime.



Figure 35. *Bryum argenteum*, a species with caducous tips but spores that often fail to germinate. Photo by George Shepherd, through Flickr Creative Commons.

Leaves and Stems

Peter Poschlod (pers. comm. 6 March 2013) considers fragmentation to be the most important dispersal diaspore in peatlands, citing the absence of *Sphagnum* spores in traps, but the frequent presence of vegetative fragments (Poschlod 1995). Furthermore, he has regenerated protonemata and shoots from leaf fragments of both *Sphagnum* from peatlands (Poschlod & Pfadenhauer 1989) and brown mosses from fens (Poschlod & Schrag 1990).

In most cases, regeneration from fragments starts with a protonema. Longton and Schuster (1983) reported that even apparently dead or dark, moribund lower shoots of *Pleurozium schreberi* (Figure 5) and *Bryum argenteum* (Figure 35) are capable of producing protonemata. Clymo and Duckett (1986) likewise reported the development of protonemata and/or shoots from lower shoot tissues that appeared to be dead or moribund. Using cores from at least 30 cm depth of *Sphagnum papillosum* (Figure 36), *S. magellanicum* (Figure 5), and *S. recurvum* (Figure 37) they were able to culture numerous new shoots. They estimated that the fragments in the cores were 25-60 years old. The growths appeared to arise from both fragments and spores, with the latter producing protonemata first. Nevertheless, some protonemata arose directly from old stems, whereas most of the growths from fragments directly produced stems and leaves. Regeneration required both light and air, explaining the lack of growth prior to removal through coring. These cores also gave rise to five species of leafy liverworts, but it is unclear if these came from fragments, gemmae, or spores.

Polytrichum species seemed to be inalcitrant to growth from leaf fragments, but in 1980, Wilmot-Dear succeeded in demonstrating regeneration from leaves in four species of the former *Polytrichum*, growing them at 20°C in a 12:12 light:dark cycle. *Polytrichum commune* (Figure 38), *P. juniperinum* (Figure 32), and *Polytrichastrum formosum* (Figure 39) developed long, much-branched secondary protonemata that produced buds. *Pogonatum urnigerum* (Figure 40) directly developed buds with no initial protonema. *Polytrichum piliferum* (Figure 41) produced short, unbranched protonemata, each with a single terminal bud. These regenerants arose

primarily from the large cells at the bases of lamellae, but some arose from the basal cells of the lamellae themselves. In *Pogonatum urnigerum* regeneration tended to decrease from the tip to the base of the leaf, whereas in *Polytrichum* and *Polytrichastrum* it decreased from base to tip. Only *Pogonatum aloides* (Figure 42), a species with persistent protonemata, did not regenerate from leaves. Wilmot-Dear advised that more experiments should be conducted on temperature prior to regeneration. *Atrichum* seems to regenerate from leaves rather easily. Gemmell (1953) reported leaf regeneration in *Atrichum undulatum* (Figure 43). I have seen it in *Atrichum angustatum* (Figure 44).



Figure 36. *Sphagnum papillosum*, a species that can regenerate from 30 cm cores. Photo by Michael Lüth, with permission.



Figure 37. *Sphagnum recurvum*, a species that can regenerate from 30 cm cores. Photo by Malcolm Storey, <www.discoverlife.com>, through Creative Commons.



Figure 38. *Polytrichum commune*, a species that can grow from leaf fragments. Photo by James K Lindsey, with permission.



Figure 39. *Polytrichastrum formosum*, a species that can grow from leaf fragments. Photo by James K. Lindsey, with permission.



Figure 40. *Pogonatum urnigerum*, a species in which regeneration decreases from apex to base. Photo by David Holyoak, with permission.



Figure 41. *Polytrichum piliferum*, a species that regenerates protonemata from leaves. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

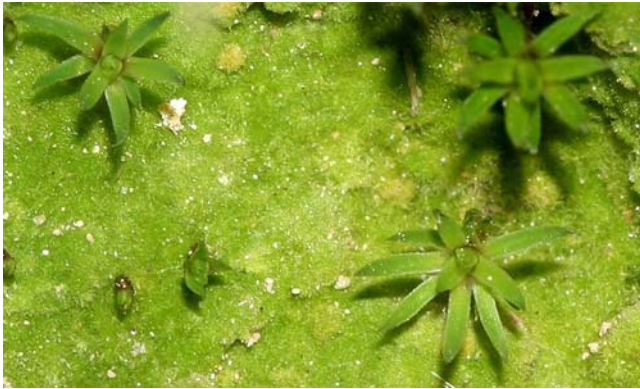


Figure 42. *Pogonatum aloides* with persistent protonemata. Photo by Walter Obermayer, with permission.



Figure 43. *Atrichum undulatum* from Gratiot River, MI, USA. These leaves can grow new plants from fragments. Photo by Janice Glime.



Figure 44. *Atrichum angustatum* with dry plants, protonemata, and buds. Photo by Janice Glime.

Newton (1972) likewise found differences in regeneration from detached leaves in *Mniaceae* species. Those of *Plagiomnium undulatum* (Figure 45)

experienced more rapid regeneration than did *Mnium hornum* (Figure 46). Fragments of both species survived frost before and during regeneration. But males failed to survive desiccation of young gametophyte regenerants from leaves, whereas 77% of the females survived.



Figure 45. *Plagiomnium undulatum*, a species with relatively rapid regeneration from detached leaves. Photo by Hermann Schachner, through creative Commons.



Figure 46. *Mnium hornum*, a species with somewhat slower regeneration from detached leaves. Photo by Bob Klips, with permission.

Early reports of regeneration from deciduous leaves or branches of leafy liverworts are provided by Cavers (1903) and Watson (1964, p. 94). I have observed the development of a young plant from a leaf in the stream-dwelling leafy liverwort *Scapania undulata* (Figure 47-Figure 48; Glime 1970). In this case, some of the plantlets developed from the center of the leaf while it was still attached to a stem fragment (Figure 48). This was not an isolated incident – several such plantlets or buds were collected in debris in drift nets being used to capture stream insects. It is interesting that this collection occurred on 1 March in Plymouth, NH, USA, before the spring melt. At this time most of the plants would be completely submerged and the stream would typically have a moderate flow from intermittent snow melt. Greatest stream flow usually occurs in this area in early April, providing a dispersal means for the plantlets. The species typically grows submersed or on rocks where it is kept moist most of the year by flowing water that splashes against the rocks. *Bazzania denudata* (Figure 49) develops plantlets on normal leaves still adhering to the plant (see Figure 50) (Fulford 1936), as in the case of *Scapania undulata* (Figure 47-Figure 48). *Plagiochila* (Figure 51), on the

other hand, can form similar growths, but these usually occur on deciduous leaves (Schuster 1960, 1966).



Figure 47. *Scapania undulata* in a typical habitat on a rock in a stream where it is nearly always wet. Moving water can easily break off fragments in this location. Photo by Dick Haaksma, with permission.

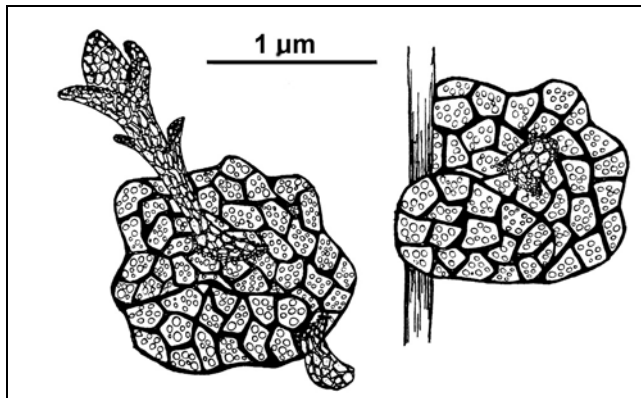


Figure 48. Detached leaf (left) with two developing plantlets and attached leaf (right) with beginning plantlet on *Scapania undulata*. Drawing courtesy of Flora Mace.



Figure 49. *Bazzania denudata*, a leafy liverwort that produces plantlets from normal leaves, but that also has fragile thin branches (shown here) projecting from beneath the stems and looking denuded. Photo from UBC Botany website, with permission.

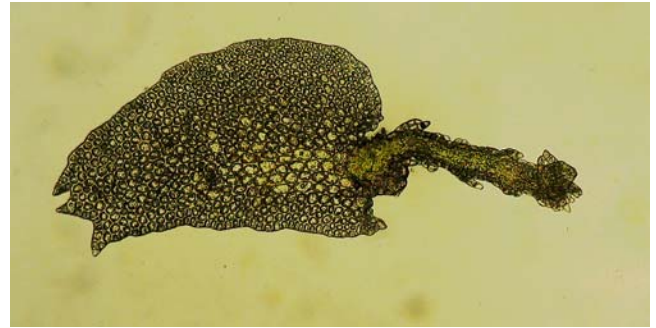


Figure 50. *Bazzania adnexa* leaf fragment with germling. Photo by Tom Thekathyl, with permission.



Figure 51. *Plagiochila asplenioides*, member of a genus that forms growths on its deciduous leaves. Photo by Dick Haaksma, with permission.

Herbarium specimens often are not as dead as they look, and even bryophytes in nature in desert types of habitats can remain desiccated for many years. Maheu (1922) rehydrated *Syntrichia ruralis* (Figure 52) after 14 years of continuous desiccation. The shoots of this species regenerated from their leaves.



Figure 52. *Syntrichia ruralis* hydrated, a species that regenerated from leaves after 14 years of desiccation. Photo by Misha Ignatov, with permission.

Stark *et al.* (2004) found that dried plants do not regenerate as quickly as fresh material. In the desert moss *Syntrichia caninervis* (Figure 53), fresh material

regenerated in 3-14 days (Figure 54). They used juvenile, green, yellow-green, and brown leaves, representing 0, 2, 6, and 12 years old respectively, to determine regeneration. The 0-2-year-old leaves had somewhat greater viability, regenerated more quickly, and extended their protonemal filaments farther in the 58 days of the experiment. They likewise produced shoots more quickly and accumulated a greater biomass. They also found that female leaves were more likely to produce a shoot than were male leaves. The sexes did not differ in time required to produce a protonema, linear extension of the protonema, or in rate of biomass accumulation. Nevertheless, protonemata derived from male leaves tended to emerge more quickly and produce greater total biomass, ultimately resulting in predominately protonemata. As a consequence, females had a higher success of shoot production, perhaps explaining rarity of males in *S. caninervis*.



Figure 53. *Syntrichia caninervis*, a species that is very desiccation tolerant and regenerates from leaves. Photo by John Game, through Creative Commons.



Figure 54. *Syntrichia caninervis* regeneration from leaf. Photo courtesy of Lloyd Stark.

Protonemata

Protonemata have been largely ignored in the ecology of bryophytes. This is not surprising due to their inconspicuous nature, difficulty in identification, and often short life. But Pasiché Lisboa (2014) has contributed to our knowledge by studying their dispersal potential in the moss *Callicosteta belangeriana* and *Taxiphyllum taxirameum* (Figure 55). Spores from wild-collected capsules were cultured axenically to get protonemata in the lab. These protonemata were placed on cardboard and splashed by three sequential drops of dyed water from 1 and 2 m height. This resulted in dispersal up to 80 cm, and it was more likely that a protonema hit by a drop would move than that it would remain stationary. These dispersed protonemata had a high survival rate, and even though most stayed within 10-12 cm, it provides an additional means for a colony to spread. I do wonder if the same dispersal would occur from soil instead of cardboard.



Figure 55. *Taxiphyllum taxirameum* with capsule, a species for which raindrop dispersal of spores has been demonstrated up to 80 cm. Photo by Bob Klips, with permission.

Perianths

But leaves and branches are not the only dispersal units through fragmentation. In *Lophozia* (= *Gymnocolea*) *inflata* (Figure 56), non-fertile **perianths** (leaves surrounding female reproductive structures) become more globose and are shorter than the fertile ones, and they develop a line of dehiscence where they are constricted at the base (Schuster 1966). Almost any disturbance will break them free. On dry days, these may drop to the ground, but more typically, when they are struck by raindrops, the perianths become free, or may already be free, and with their included air bubble they easily float. Such perianths then are carried away by water. But one could argue equally well that this light weight would permit them to be carried by wind should they be broken free on a dry and windy day. However, there is little documentation of regeneration from liverwort parts, so we can only guess that these perianths are able to form new plants. Perianths of *Chonecolea doellingeri* likewise are easily dislodged, but these do not become inflated (Schuster 1966).

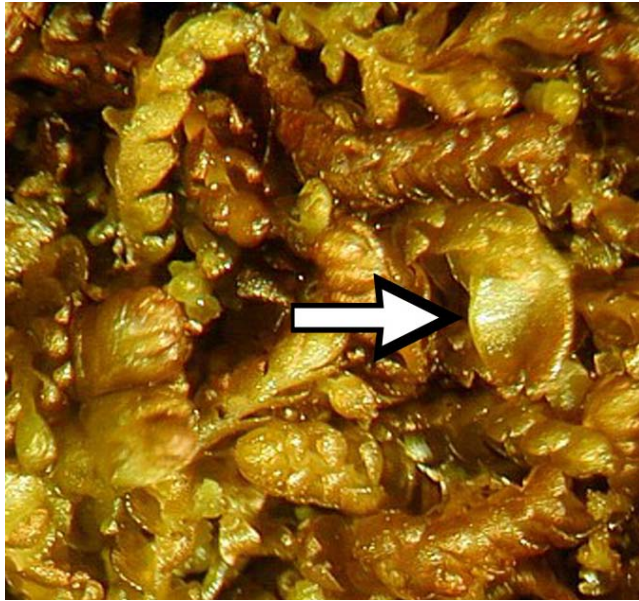


Figure 56. Perianth (arrow) of *Lophozia* (=Gymnocolea) *inflata*. Photo by Michael Lüth, with permission.

Calyptrae

Britton (1902) reported that *Schistophyllum julianus* (as *Octodiceras julianum*) (Figure 57) is able to regenerate from its calyptra, producing protonemata. The capsules of this species fall off just before maturity while they are still green and the calyptra is still attached. Together they are able to float, hence creating a potential dispersal unit of the calyptra. Its vegetative dispersal capabilities may account for its widespread occurrence in many kinds and locations of aquatic habitats.



Figure 57. *Schistophyllum julianus*, a species that can regenerate from its calyptra. Photo by Jan-Peter Frahm, with permission.

Wynne and Budke (2012) took the calyptrae one step further in *Funaria hygrometrica* (Figure 58). They looked at the ability of the calyptra to produce protonemata as a function of time and discovered several things: 1) The calyptrae remain alive and capable of producing protonemata for at least 28 days after detachment from the capsule; 2) the younger calyptrae produced significantly more protonemata than the oldest of three developmental stages.



Figure 58. *Funaria hygrometrica* young sporophytes with calyptrae. Photo by Michael Lüth, with permission.

Involucres

The **involucre** (protective sheath originating from thallus and surrounding single gametangium or sporophyte) is not a structure one would normally consider as a dispersal unit. Nevertheless, in *Metzgeria* (Figure 59), this seems to be the case (Kuwahara 1968, 1973). Eight species in this genus, including *M. acuminata*, *M. agnewii*, *M. arborescens*, *M. filicina*, *Echinomitrium* (=Metzgeria) *furcata* (Figure 60), *M. grollei*, *M. imberbis*, and *M. liebmanniana*, all have demonstrated the ability to grow branches from female involucres into normal vegetative thallus. These liverworts have come from Europe, Africa, South America, and North America, suggesting that the phenomenon might be present in other taxa that produce involucres. Since these are early papers, it is likely that other examples are known. But do these have any significance for fragmentation and dispersal?



Figure 59. *Metzgeria conjugata* with sporophyte and basal involucre. Photo from Botany website, University of British Columbia, BC, Canada, with permission.



Figure 60. *Metzgeria furcata*, a species that can regenerate from the involucre. Photo by Des Callaghan, with permission.



Figure 62. *Rhodobryum roseum*, a moss in which paraphyses can develop protonemata. Photo by Hermann Schachner, through GNU Free Documentation.

Paraphyses

Many mosses produce paraphyses that surround the antheridia and archegonia. These are usually considered to help maintain more constant moisture conditions than would be possible without them, help to squeeze sperm out of the antheridia, and may also function to protect against frost, solar radiation, and herbivore damage. But the presence of chlorophyll in a structure that would not seem to need it caused Correns (1890) and Hill (1903) to suspect that they might also serve as propagula. Hill even observed protonema-like branching in paraphyses (Figure 61) from *Rhodobryum roseum* (Figure 62-Figure 63). But early attempts to actually grow new plants from these paraphyses failed (Heald 1898; LaRue 1930).

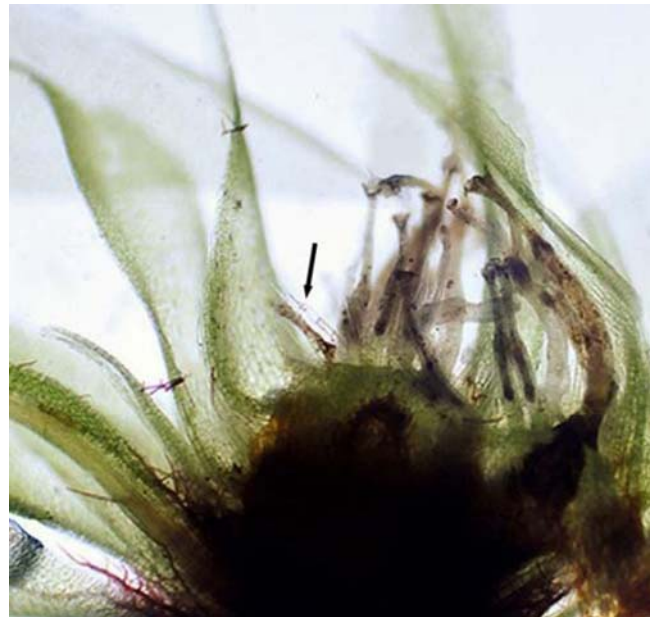


Figure 63. *Rhodobryum roseum* perichaetium. Arrow indicates paraphysis. Photo by George J. Shepherd, through Creative Commons.

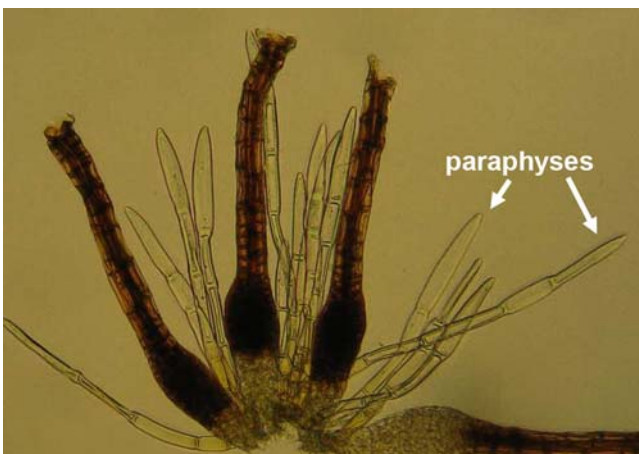


Figure 61. *Zygodon intermedius* archegonia among paraphyses. Photo by Tom Thekathyil, with permission.

Finally, Reese (1955), also convinced that a regenerative function was implied by the presence of chlorophyll in the paraphyses, managed to culture paraphyses of three species and successfully produce regeneration: *Ptychostomum* (= *Bryum*) *capillare* (Figure 7) 10%; *Aulacomnium palustre* (Figure 64) 12.5%; *Funaria hygrometrica* (Figure 65) 25%. *Ptychostomum capillare* and *Funaria hygrometrica* required only one month for the first evidence of regeneration, whereas *Aulacomnium palustre* required two months. Reese suggested that the ease of obtaining regenerants from these three mosses suggests that other mosses with green paraphyses might also regenerate in this way. But this leaves one question remaining, how are they dispersed?



Figure 64. *Aulacomnium palustre* in MI, USA. Photo by Janice Glime.



Figure 65. *Funaria hygrometrica* with young sporophytes. Photo by Andrew Spink, with permission.

Falling Epiphytes

In the tropics, where epiphytes abound, bryophytes can fall from the canopy. Within dense canopies, these bryophytes can fall to another branch that is within their tolerance range for light, temperature, and humidity. Others will fall to the ground. Clumps of plants in the Neotropics ranged in size from 90 cm³ to 36,000 cm³ with the number of individual plants per clump ranging 2-9 (Matelson *et al.* 1993). Unfortunately for us, data for bryophytes were not separated from the general assessment. Matelson *et al.* found that these falling epiphytes can contribute to the NH₄⁺ and K⁺ of the forest floor. There were no significant differences in longevity among the eight plant categories (bryophytes being one category), suggesting that perhaps some of the bryophytes could continue to live and possibly be re-dispersed by wind or animals.

Moss Balls

Some fragments get dispersed by snow and ice and may even blow around as moss balls on glaciers. McDaniel and Miller (2000) reported both bryophyte and vascular plant fragments in late-spring snowbeds in the Adirondack Mountains, NY, USA. The alpine fragment diversity far exceeded that from a forested site, and the bryophyte diversity exceeded that of the vascular plants. Among the bryophytes, 82% were sufficiently healthy and complete to permit identification to genus or species. An interesting revelation was the presence of liverworts from the alpine samples, suggesting that their absence from late-

glacial sediments may be due to the fossilization process (taphonomy) rather than their absence in the flora or their inability to disperse by fragments. Although rare, some of the fragments in the alpine areas came from lower elevation balsam fir and red spruce-balsam fir forests. Fragments deposited on the snow would be available for immediate establishment when the snow melted, with cool temperatures and plenty of water to get started. The bryophytes will be there when the glaciers melt.

Cushions of mosses from large basalt outcrops can create moss balls when they become detached from their substrate (Pérez 2010), particularly due to activity of the Dark-rumped Petrels (*Pterodroma phaeopygia*) that burrow to make nests under outcrops. Such detachment can be facilitated by rainfall, desiccation, wind, frost, and animal disturbance. These balls can form as the clumps are transported down steep slopes (26-34°) by geomorphic processes such as frost (especially needle ice activity), runoff, and wind. At the Haleakala crater, Maui, Hawaii, USA, these balls contained *Grimmia trichophylla* (Figure 66) and *G. torquata* (Figure 67). Pérez found that the larger mosses tended to become flattened because they were less disturbed by needle ice, hence remaining immobile for longer periods of time. These potential moss balls generally moved less than 100 cm (83%); only 5% moved 200-839 cm. Trapping of dust grains and small soil particles, combined with water-holding capacity of the mosses, created a greater water storage capacity in these balls (310%) compared to that in the soils of the site (16.8%). Pérez interpreted this as a self-replicating dispersal system on these slopes.



Figure 66. *Grimmia trichophylla* on a boulder. Clumps such as this are easily broken off and can become moss balls. Photo by Michael Lüth, with permission.



Figure 67. *Grimmia torquata*. Once free a clump can become a moss ball; lower branches grow toward the center of an upside down plant. Photo by Michael Lüth, with permission.

I have seen moss balls that fell from the talus slopes near the Red River in New Mexico, USA. There were numerous balls on the ground near the base of the slope, some quite rounded and others irregular in shape (Figure 69-Figure 68).



Figure 68. Detached moss ball formed by rolling down the talus slope shown in Figure 69. Photo by Janice Glime.



Figure 69. Talus slope near the Red River, New Mexico, USA, a source of mosses that roll down the slopes and across the valley below, breaking off tips and becoming rounded moss balls. Photo by Janice Glime.

Animals – Breaking or Ingesting Bryophytes

Some fragments have a little help from the animals in the vicinity. We are finding an increasing number of animals that ingest bryophytes, including insects, earthworms, molluscs, rodents, and occasionally larger mammals. (See next subchapter.)

Extreme Environments

In extreme environments, fragments may be important in dispersal. They can be produced under the most harsh conditions and be blown around in an arrested state until landing in a suitable microhabitat.

Antarctic & Arctic

On the continent of Antarctica, only three bryophytes were known to produce sporophytes: *Bryum pseudotriquetrum* (as *Bryum algens*; Figure 70) (Filson & Willis 1975), *Hennediella heimii* (as *Bryum antarcticum*; Figure 71) (Kanda 1981), and *Grimmia trichophylla* (Figure 66; Selkirk 1984). However, birds and other animals scratching among the plants dislodge numerous fragments (Selkirk 1984). When Selkirk (1984) set out Tauber traps (Tauber 1974) to collect the diaspores on the surface of the snow in the Antarctic, she found that only two species had been dispersed by specialized structures: *Ulota phyllantha* (Figure 72) by gemmae (Figure 72-Figure 74) and *Dicranella cardotii* by stem tips. Most of the plants, however, had been dispersed by various fragments of leaves and stems. She further verified that many of these moss taxa were actually growing from vegetative fragments at all the types of sites she observed where bare, colonizable areas were available.



Figure 70. *Bryum pseudotriquetrum*, one of three bryophytes known to produce sporophytes in the Antarctic. Photo by David T. Holyoak, with permission.



Figure 71. *Hennediella heimii* with capsules, a species that produces capsules in the Antarctic. Photo by David T. Holyoak, with permission.



Figure 72. Brown gemmae of *Ulota phyllantha*, a dispersal unit found in Tauber traps in the Antarctic. Photo by Michael Lüth, with permission.

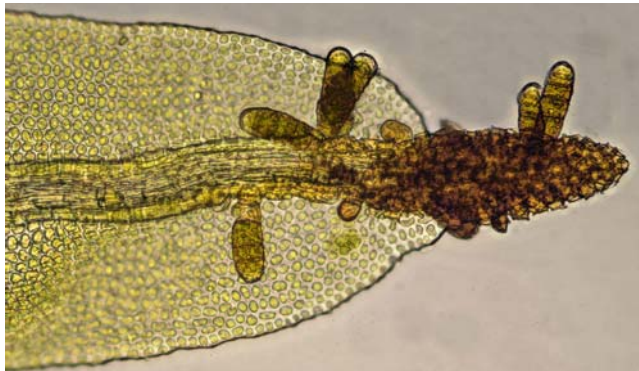


Figure 73. *Ulota phyllantha* gemmae at tip of leaf. Photo by Dick Haaksma, with permission.

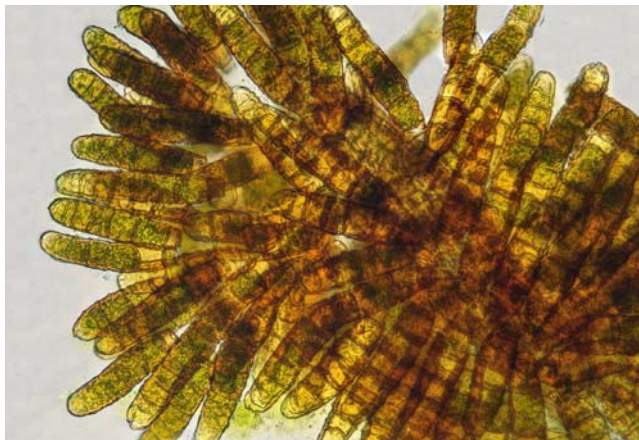


Figure 74. *Ulota phyllantha* gemmae at tip of leaf. Photo by Dick Haaksma, with permission.

In Arctic Canada, Miller and Howe Ambrose (1976) estimated a total of 33,820 bryophyte fragments per cubic meter of granular snow! Of these, 97% were less than 2.25 mm, so small that airborne dispersal was likely. They found that almost all the viable fragments were leaf-bearing moss stem tips. Based on their experiments and the number of fragments available, they estimated that over 4000 viable propagules occurred per cubic meter of granular snow. They suggest that the same winds that serve to disperse these fragments serve as the agent to break the fragments from the plants. Cold air and desiccating conditions make the plants more fragile and contribute to the breakage.

Alpine

Many bryophytes seldom or never produce sporophytes in harsh environments such as that of alpine summits, requiring them to rely on asexual means for reproduction and dispersal. Robinson and Miller (2010) compared two species of *Sphagnum* from the Adirondack Mountains and other high altitude sites in eastern North America. These two species [*S. pylaesii* (Figure 75), *S. tenellum* (Figure 76)] live in similar habitats, but their life strategies differ. Robinson and Miller used 17 microsatellite loci to infer dispersal from the gene flow estimates. Branch fragments of *S. pylaesii* were coated with UV-fluorescent dye and released from two alpine summits. Fragments were located after 12 and 24 h and 1 week using UV LED light sources in the evening. Both species exhibited more genetic variation than expected. However, the species differed, with *S. pylaesii* having high differentiation and low gene flow between populations throughout its North American distribution. *Sphagnum tenellum* was less differentiated and showed higher levels of gene flow. Robinson and Miller concluded that fragments played an important role in transport both on summits and to other alpine summits.



Figure 75. *Sphagnum pylaesii*, a species that can be dispersed by branch fragments. Photo by Michael Lüth, with permission.



Figure 76. *Sphagnum tenellum* with capsules. This is a species that exhibits greater gene flow than *S. pylaesii*, perhaps due to its capsule production. Photo by Dick Haaksma, with permission.

Vegetative Diaspores

Correns (1899) examined 915 types of mosses with **vegetative diaspores** (specialized propagula of Longton and Schuster). Since then, usage of terminology has

diverged among the countries of the world, and even within one country. In the recent *Glossarium Polyglottum Bryologiae* (Magill 1990), bryologists from around the world attempted to standardize terminology. In that edition, Magill used the concept of Goebel (1905) that divided vegetative diaspores into two groups based on their development at germination. He applied the term **propagula** to those diaspores that have an apical cell and can grow directly into a leafy shoot if the apical cell is reactivated (Figure 78, Figure 90). Unfortunately, this definition is clouded by its impracticality and because even these diaspores usually produce protonemata.

Köckinger and Kucera (2007) considered that *Barbula amplexifolia* (Figure 77) reached the Austrian Alps by vegetative gemmae across the cold Pleistocene steppes from Central Asia. They support this conclusion by the absence of male plants and sporophytes in the Alps and the low level of morphological and anatomical variability. They suggest that extensive road construction through the forests may be facilitating their recent increase in distribution.



Figure 77. *Barbula amplexifolia* with capsules in India. Photo by Michael Lüth, with permission.



Figure 78. Deciduous branches (**propagula**) of the moss *Campylopus pilifer*, representing a common means for its reproduction. Photo by Michael Lüth, with permission.

Magill (1990) likewise used the concept of Goebel to define **gemmae** as vegetative diaspores with no apical cell and that always must begin growth with a protonemal phase (Figure 19, Figure 90). These units then include caducous leaves and endogenous gemmae, as well as those specialized, oval, round, or irregularly shaped structures we have always called gemmae in the strictest sense.

Among the **propagula**, Imura and Iwatsuki (1990) identified four aboveground types:

1. **Deciduous shoot apices** (Figure 35, Figure 79) result from an area weakened by a cleavage in the cell walls. These often already have rhizoidal initials at their basal parts. Such shoot apices occur in *Bryum argenteum* (Figure 35) and *Campylopus sinensis* (= *C. japonicus*) (Figure 79).



Figure 79. *Campylopus sinensis* (= *C. japonicus*) with broken tips. Photo from Hiroshima University website, with permission.

2. **Caducous branchlets** (caducous = deciduous) seem like deciduous shoot apices, except that they are branchlike structures with minute leaves and are attached to the parent plant by one-celled stalks. A good example of these is in *Pterigynandrum filiforme* (Figure 80; Bergamini 2006). Although such branches are not common among pleurocarpous bryophytes, they can also be found in *Pseudotaxiphyllum* (= *Isopterygium*) *elegans* (Figure 81), *Leucodon sciuroides* (Figure 82), *Platygyrium repens* (Figure 83-Figure 84), and *Pseudoleskeella nervosa* (Figure 85).



Figure 80. *Pterigynandrum filiforme*. Photo by Dick Haaksma, with permission.



Figure 81. *Pseudotaxiphyllum* (=Isopterygium) *elegans* with caducous filiform branches that serve as propagules. Photo by Jan-Peter Frahm, with permission.



Figure 82. *Leucodon sciurioides* var. *sciurioides*. Photo by David Holyoak, with permission.



Figure 83. *Platygryium repens* with bulbils at tips of branches. Photo by Dick Haaksma, with permission.

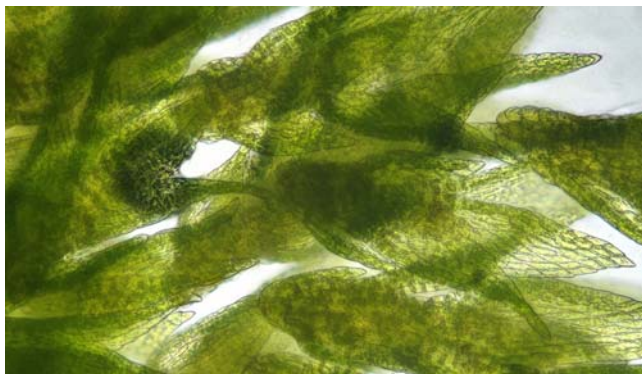


Figure 84. Microscope view of *Platygryium repens* bulbil branches. Photo by Dick Haaksma, with permission.



Figure 85. *Pseudoleskeella nervosa* showing bulbils (caducous branchlets) at branch tips. Photo by Hermann Schachner, through Creative Commons.

3. **Flagella** are slender branches with reduced leaves and occur in the axils of upper leaves. The basal portion is multicellular, thus separating them from caducous branchlets. These are common in *Dicranum flagellare* (Figure 23).
4. **Bulbils** (Figure 86-Figure 90) usually occur on one-celled, short stalks and have what appear to be partially developed leaves. Some are round and bulb-like, others are thread-like. They are common in *Pohlia* (Figure 86-Figure 89).



Figure 86. *Pohlia flexuosa* with flagelliform bulbils. Photo by Jan-Peter Frahm, with permission.



Figure 87. *Pohlia bulbifera*. Photo by David T. Holyoak, with permission.



Figure 88. *Pohlia bulbifera* bulbils in leaf axil. Photo by Des Callaghan, with permission.



Figure 89. *Pohlia filum* with bulbils in Europe. Photo by Michael Lüth, with permission.

Gemmae can be filamentous, spindle-shaped, globular, discoid, or multi-horned (Figure 90). They occur on various parts of the gametophyte and sometimes have pale, thin-walled cells at the base. Protonemal and rhizoidal "gemmae" are usually labelled **bulbils** on materials from biological supply houses. Two types of gemmae can be identified based on their origin on the plant:

1. **Caducous leaves** are very specialized leaves of reduced size that may or may not differ from normal leaves in basic structure. In *Aulacomnium*, most of the taxa produce special branches with gemmae (caducous leaves) that are easily detached, reduced leaves (Imura *et al.* 1991). In *Campylopus fragilis* (Figure 93-Figure 94) and *Syntrichia laevipilum* (as *Tortula pagorum*; Figure 91-Figure 92), the caducous leaves are on short branches at the axils of upper leaves (Imura & Iwatsuki 1990). *Thuidium cymbifolium* (Figure 95) produces caducous flagella (Akiyama 2009).

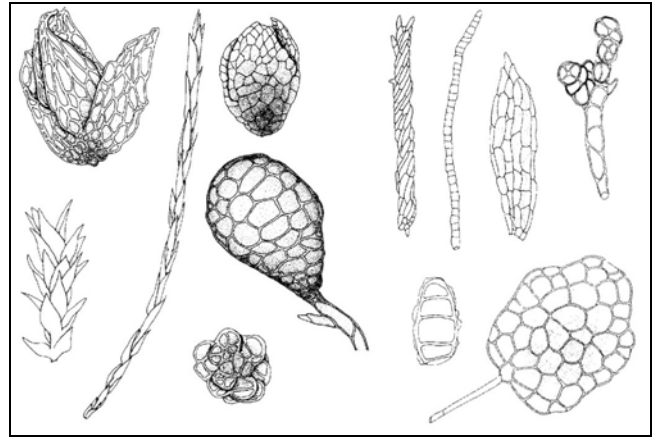


Figure 90. Propagula and gemmae of selected bryophytes. Redrawn from Imura and Iwatsuki (1990).



Figure 91. *Syntrichia laevipilum* (= *Tortula pagorum*) with caducous leaves in the axils of upper leaves. Photo by Robert Klips, with permission.

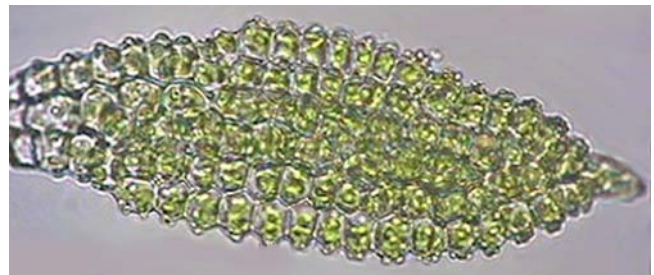


Figure 92. Caducous leaf gemma from axils of upper leaves of *Syntrichia laevipilum*. Photo by Paul Davison, with permission.



Figure 93. *Campylopus fragilis* with short branches having caducous leaves in the axils of upper leaves. Photo by David T. Holyoak, with permission.



Figure 94. *Campylopus fragilis* with caducous leaves and branches. Photo by Jan-Peter Frahm, with permission.



Figure 95. *Thuidium cymbifolium* with capsules, a species that forms caducous flagella for asexual reproduction. Photo by Li Zhang, with permission.

2. **Endogenous gemmae** (Figure 96-Figure 106) are produced inside a cell initial. Most of the taxa among the mosses with these structures are in the **Grimmiaceae**, but they are common among the **liverworts**, often occurring as patches of non-green color at leaf tips or margins.



Figure 96. *Heterogemma* (=Lophozia) *capitata* leafy plant with sporophyte; this species produces endogenous gemmae (Figure 97). Photo by Jan-Peter Frahm, with permission.



Figure 97. *Heterogemma* (=Lophozia) *capitata* with endogenous gemmae on leaf margin. Photo modified from web site of Paul Davison <www2.una.edu/pdavis/bryophytes.htm>, with permission.



Figure 98. *Scapania nemorea* in Europe showing apical gemmae. Photo by Michael Lüth, with permission.



Figure 99. *Scapania nemorea* showing mature apical gemmae. Photo by Dick Haaksma, with permission.



Figure 100. *Scapania nemorea* gemmae on leaf. Photo by Dick Haaksma, with permission.



Figure 101. *Scapania nemorea* gemmae on leaf margin. Photo by Paul Davison, with permission.



Figure 102. *Scapania nemorea* leaf gemmae. Photo by Dick Haaksma, with permission.



Figure 103. *Lophozia ventricosa* with leaf gemmae. Photo by Jan-Peter Frahm, with permission.



Figure 104. *Jubula* (= *Radula*) *complanata* with gemmae on leaf margins. Photo by Walter Obermayer, with permission.



Figure 105. *Jubula* (= *Radula*) *complanata* gemmae. Photo by Walter Obermayer, with permission.

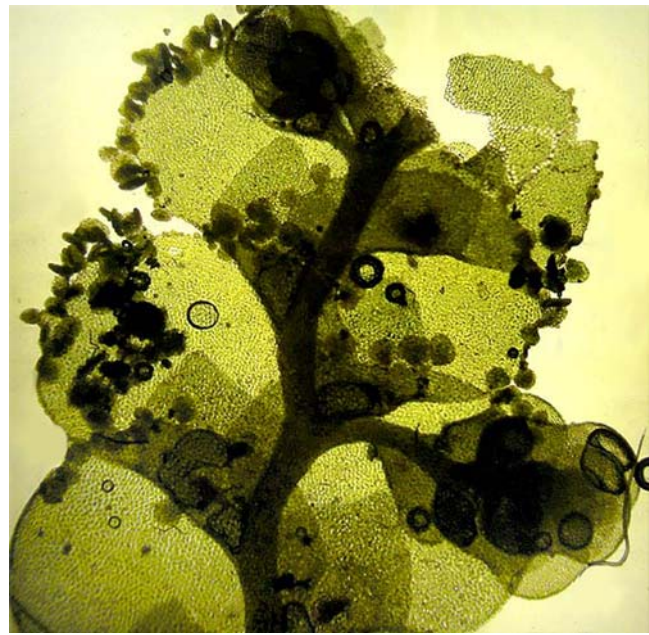


Figure 106. *Jubula* (= *Radula*) *complanata* leaves with gemmae. Photo by Walter Obermayer, with permission.

Stem and Leaf Gemmae

As one might expect, at least in some cases, the environmental conditions can have a strong effect on forms and numbers of gemmae. For example, the species *Bryum dichotomum* has several forms that previously have been named as different species (Dolnik 2006). These species, including the synonym *B. bicolor* (Figure 107), have been separated based on the forms and numbers of gemmae. Dolnik germinated the bulbils in culture in the greenhouse under a variety of conditions. In the form of *B. dichotomum* identified as its synonym *B. barnesii* (Figure 108-Figure 109), environmental conditions had no effect on number of bulbils per leaf axil, but the shape varied with seasonal variability, causing taxonomists to initially consider them to be different species. Both these bulbils and those developing on protonemata can float for several days and remain viable, providing a potential means of long-distance dispersal to locations along streams and shorelines where water levels vary.



Figure 107. *Bryum dichotomum* (*B. bicolor* form). Photo by Michael Lüth, with permission.



Figure 108. *Bryum dichotomum* (*B. barnesii* form) with bulbils in leaf axils. Photo by Kristian Peters, with permission.



Figure 109. *Bryum dichotomum* (*B. barnesii* form) bulbil from leaf axils. Photo by Kristian Peters, with permission.

In the genus *Fossombronia*, two species are known to produce budlike vegetative propagules from leaf cells (Zhang *et al.* 2003). In South Africa, *Fossombronia gemmifera* has this behavior (Cargill 2000). In Australia, sterile plants of *Fossombronia cerebriformis* produce adaxial leaf gemmae at the bases of leaves (Scott & Pike 1984).

Newton (2002) found flagelliform propagules that were ready for dispersal in *Pilotrichella flexilis* (Figure 110). These developed from primordia in leaf axils where they had minute juvenile leaves and in some cases rhizoids were present on some branchlets. Although miniature branches often serve as propagules, this is the first time they are known to develop from moss leaves (Schuster 1966). In *P. flexilis* these develop directly from the alar cells and do not develop protonemata. The phenomenon of developing miniature shoots from leaf cells is known among the liverworts in the genus *Plagiochila*.

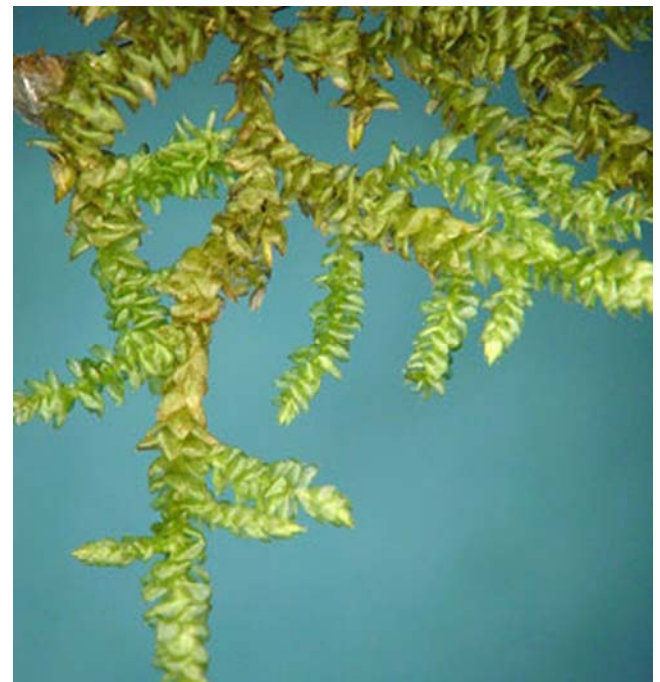


Figure 110. *Pilotrichella flexilis*, a species that has flagelliform propagules (miniature branches) developed from primordia in leaf axils. Photo by Claudio Delgadillo Moya, with permission.

Rhizoidal Gemmae

As I began working on this section, I quickly realized I had a nomenclature problem. I had a number of images of rhizoidal tubers – no problem there. But I also had a number labelled **rhizoidal gemmae**, all from bryologists. All but one of these gemma images resembled the tubers. After consulting the *Glossarium Polyglottum Bryologiae*, I was comforted to learn that in mosses, rhizoidal tubers were defined as gemmae born on rhizoids. But one of these images was quite different, that of *Fissidens macaoensis* (Figure 111-Figure 113). In this species, the rhizoidal gemmae are elongate filaments that are narrow at the base and expand toward the tips (Figure 112; Zhang & Hong 2011). And it develops **rhizoidal tubers** (Figure 113) at the same time, a seemingly unique character among mosses. Zhang and Hong suggest that these two types of

gemmae on the soil surface could be an adaptation that permits easy dispersal up to several hundred meters during floods created during the typhoon season in Macao, China.



Figure 111. *Fissidens macaoensis*, a tiny species with both rhizoidal tubers and rhizoidal gemmae at the same time. Photo by Li Zhang, with permission.

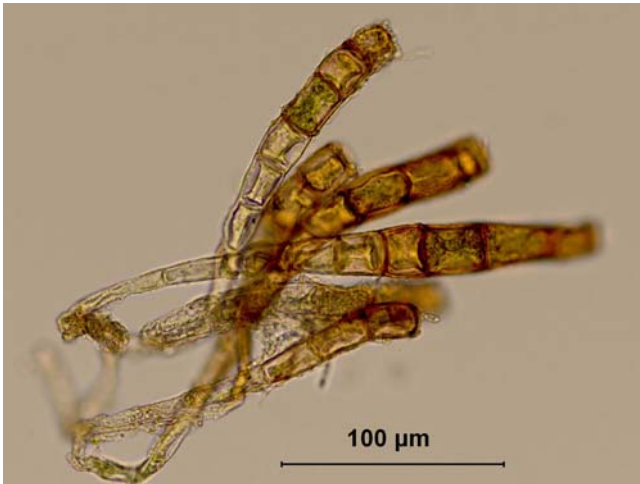


Figure 112. *Fissidens macaoensis* rhizoidal gemmae. Photo by Li Zhang, with permission.

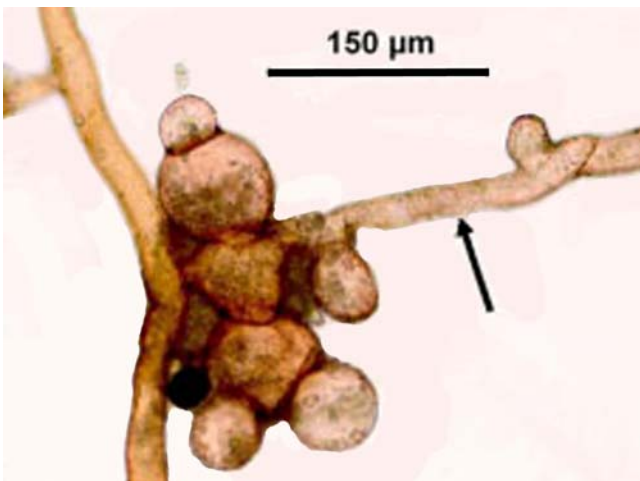


Figure 113. *Fissidens macaoensis* rhizoidal tuber. Photo by Li Zhang, with permission.

Risse (1986) observed the development from rhizoidal gemmae of *Dicranella rufescens* (Figure 114) and reviewed the rhizoidal gemmae of 82 European moss species and 3 additional ones from outside Europe (Risse 1987). Pressel *et al.* (2007) reviewed the protonemal

propagules in *Bryum* (Figure 115-Figure 116, Figure 122-Figure 125) and related genera. Lepp (2008) reports over 100 species with rhizoidal gemmae, but most likely there are many more that have not been investigated.



Figure 114. *Dicranella rufescens* with rhizoidal gemmae. Photo by David T. Holyoak, with permission.



Figure 115. *Bryum* rhizoid with gemma tubers. Photo courtesy of Javier Abaigar Martinez.

Nordhorn-Richter (1984a) discovered that many parts of bryophytes, including asexual propagules, could be distinguished with the fluorescence microscope. She found this to be especially important in finding rhizoidal tubers and other propagules in the genus *Pohlia* (Nordhorn-Richter 1984a-d, 1985, 1988).

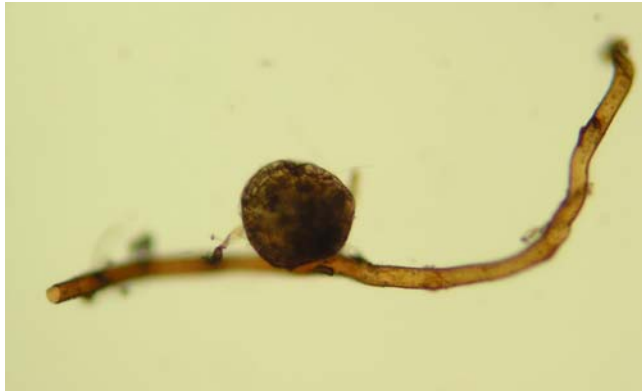


Figure 116. *Bryum* rhizoid gemma tuber. Photo courtesy of Javier Abaigar Martinez.

Whitehouse (1961) reported rhizoidal gemmae from *Hennediella* (= *Tortula*) *stanfordensis* (Figure 117) in Cornwall, Great Britain, and later Reese (1967) reported them in *Chenia leptophylla* (= *Tortula vectensis*; Figure 118-Figure 119) from North America. *Hennediella stanfordensis* forms a band nearly 1 km long on the coast near Lizard Point. Male plants seem to be absent, so this species depends on its gemmae, also chloronemal gemmae, and probably fragments. It is a winter annual, surviving the summer primarily through these rhizoidal gemmae.



Figure 117. *Hennediella stanfordensis*. Photo by Paul Wilson, with permission.



Figure 118. *Chenia leptophylla*. Photo by Jonathan Sleath, with permission.



Figure 119. *Chenia leptophylla* rhizoidal tuber. Photo by Jonathan Sleath, with permission.

Rhizoidal Tubers

Rhizoidal tubers (Figure 120-Figure 126) occur on the rhizoids and are usually filamentous, branched, or spherical and have diverse origins. Whitehouse (1966) described these for 29 species of European mosses. He considered them to be a means of survival in arable fields and a means of dispersal for taxa living by streams. These often occur on species where sporophytes are unknown. Arts (1994) reported both rhizoidal tubers and protonemal gemmae in nine species of *Ditrichum* (Figure 120-Figure 121). They are common in the genus *Bryum* (Figure 122-Figure 125), and are likewise known in *Pohlia* (Figure 126). Arts (1986a) cultivated tubers of *Fissidens dubius* (= *F. cristatus*; Figure 127) and established that they are drought resistant. The large tubers of *Campylopus pyriformis* (Figure 128) are likewise drought resistant and contain large quantities of starch (Arts 1986b). Their dark color may indicate antiherbivore compounds or may serve as a filter against light, decreasing chances of germination under a small amount of soil.



Figure 120. *Ditrichum cornubicum*, a species with rhizoidal tubers. Photo by David T. Holyoak, with permission.



Figure 121. *Ditrichum cornubicum* rhizoidal tuber. Photo by David T. Holyoak, with permission.



Figure 122. *Bryum canariense* rhizoidal tubers exposed in the soil. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

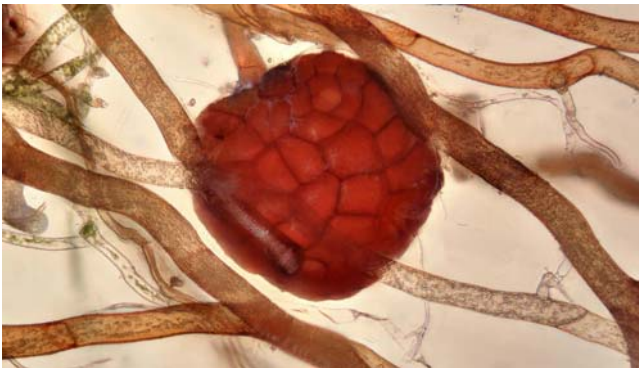


Figure 123. *Bryum bornholmense* rhizoidal tubers. Photo by Dick Haaksma, with permission.

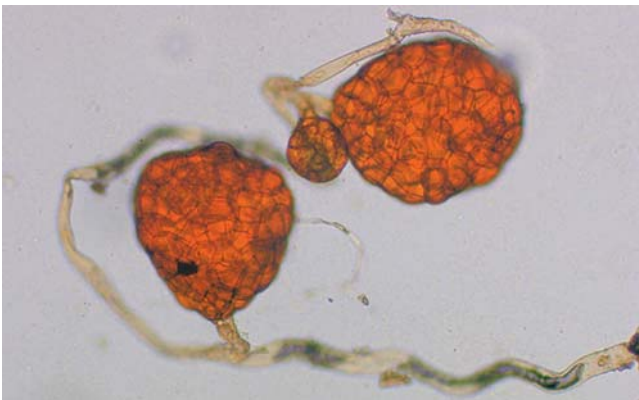


Figure 124. *Bryum tenuisetum* rhizoidal tubers. Photo by Chris Hesse, with permission.

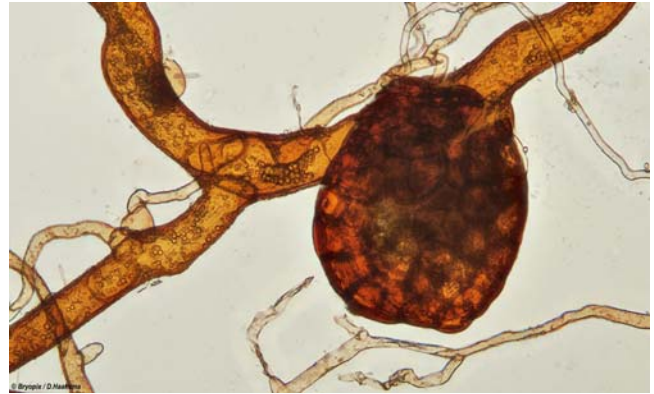


Figure 125. *Bryum torquescens* rhizoidal tuber. Dick Haaksma, with permission.



Figure 126. *Pohlia wilsonii* rhizoidal tuber. Photo by Guillermo M. Suárez.



Figure 127. *Fissidens dubius*, a species with drought-resistant rhizoidal tubers. Photo by Bernd Haynold, through Creative Commons.

Protonemal Gemmae

Because of identification difficulties, we seldom examine protonemata closely in the field. Hence, to many of us, protonemal gemmae are all but unknown. Nevertheless, Pressel *et al.* (2007) consider them to be relatively common. These protonemal gemmae occur in a variety of families. The moss *Trematodon brevicalyx* (Bruchiaceae) produces them (Dhingra & Chopra 1983) and they are known in 36 species of *Bryum* (Chopra & Rawat 1977; Pressel *et al.* 2007).

It is likely that many species have protonemal gemmae or other reproductive structures that remain to be discovered. For example, these were unknown until recently in the Splachnaceae. Following the discovery of protonemal bulbils in *Splachnum ampullaceum* (Figure 129) (Mallón *et al.* 2006), Martínez and Price (2011) studied the development of the protonemata of the epiphytic *Tayloria rudolphiana* (Figure 130), likewise a member of the Splachnaceae. In culture, they observed protonemal brood cells for the first time in this species, occurring at the ends of caulonemal filaments where they formed chains of short, somewhat thick-walled spherical cells. These brood cells developed after four months in culture and had abundant chloroplasts and some lipid droplets.



Figure 128. *Campylopus pyriformis* with caducous leaves, also producing rhizoidal tubers. Photo by Michael Lüth, with permission.



Figure 129. *Splachnum ampullaceum* with capsules. Photo by David Holyoak, with permission.



Figure 130. *Tayloria rudolphiana*, a species that produces chains of spherical protonemal brood cells at the ends of caulonemal filaments. Photo by Jan-Peter Frahm, with permission.

The production of protonemal gemmae seems to be environmentally controlled. Vashistha and Chopra (1984) found that in *Didymodon recurvus* the production of protonemal gemmae was favored by low light and high temperature, whereas high light and low temperature resulted in development of gametophore buds. This experimental observation is consistent with the assertion of Whitehouse (1980). He found that the protonemata of *Barbula trifaria*, *Gyroweisia tenuis*, and *Eucladium verticillatum*, as well as those previously reported in *Schistostega pennata* (Edwards 1978), seem to be adaptations for survival and propagation at low light intensities of deep shade. Perhaps this is a mechanism to provide an opportunity for dispersal from an unfavorable location to one with more favorable light?

Pressel and coworkers (2007) found that in culture the protonemal gemma production increased with high nutrient availability and suggested that this may be true in nature as well. They assumed that the protonemal gemmae were both less long lived and less desiccation tolerant than tubers. They suggested that these diaspores helped in initial establishment as well as local spread of the species. The role in the diaspore bank and longevity of these structures remain to be investigated.

It is interesting that development of protonemal gemmae may also be controlled by the hormone IAA (Ahmed & Lee 2010). Ahmed and Lee found that both IAA and kinetin controlled the production of gemmae vs gametophore buds in *Palustriella decipiens* (= *Cratoneuron decipiens*) cultures from chopped up gametophores, serving as concentration-based external regulators. This does not necessarily imply that the same behavior would occur from protonemata produced by spores because chopped plants could provide hormones that might not be available to a spore germling.

Liberation Mechanisms

Even the mechanisms of liberating the diaspores differ among species. Duckett and Ligrone (1992) identified five liberation mechanisms:

1. random breakage of thin-walled stalk cells
2. formation of new internal walls that separate from old

3. severance along middle lamella of basal cell with or without rounding off of cells
4. formation of highly specialized abscission (**tmema**) cells
5. breakage along intercalary region of thin-walled living cells

In contrast to these specific liberation mechanisms, rhizoidal gemmae lack any separation mechanism, being freed only by decay of the filament that has produced them.

Some bryophytes don't require any special cells or mechanisms to release fragments. For example, the leafy liverwort *Pycnolejeunea* will lose a shoot with only a light touch. Others may produce special branches that release with only a touch. This adaptation usually results from reduction in number of cells at the point of attachment. The ease-of-breakage method includes many leafy liverworts. One such species is *Lejeunea cardotii* that grows in mats on tree trunks and dead wood. Its stems produce small-leafed branches and these may in turn produce more small-leafed branches. These are fragile and break off easily. Other leafy liverworts, e.g. *Bazzania trilobata* (Figure 131), likewise get such specialized branches, often originating from under the branch.



Figure 131. *Bazzania trilobata* showing stolons with very reduced leaves. Photo by Dick Haaksma, with permission.

Protonemal Gemmae

Most of the protonemal gemmae separate from the parent **chloronema** (part of protonema giving rise to buds) by a **tmema** (abscission) cell. Other taxa with this tmema mechanism include *Mielichhoferia bryoides* and *Rhodobryum roseum* (Figure 62). Other bryophytes use **schizolysis** to detach their gemmae. This requires the splitting from the parent plant by **lysis** of the cellular connections through rupture of adjoining cell walls. Genera with this strategy include *Epipterygium* (Figure 132), *Plagiomnium* (Figure 133), *Rhizomnium* (Figure 134), and *Mnium* (Figure 135).

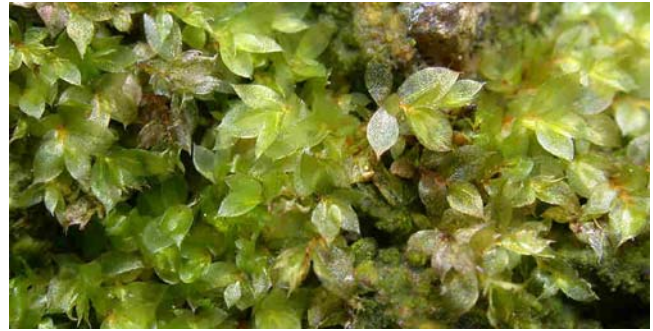


Figure 132. *Epipterygium tozeri*, representing a genus that uses lysis to disconnect its gemmae. Photo by David T. Holyoak, with permission.



Figure 133. *Plagiomnium affine*, representing a genus that uses lysis to disconnect its gemmae. Photo by Michael Lüth, with permission.



Figure 134. *Rhizomnium punctatum*, representing a genus that uses lysis to disconnect its gemmae. Photo by Li Zhang, with permission.



Figure 135. *Mnium arizonicum*, representing a genus that uses lysis to disconnect its gemmae. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Tmema

A **Tmema** (Figure 136-Figure 137) is a specialized abscission cell that permits portions of a protonema to operate independently and create a position of easy breakage (Correns 1899; Duckett & Ligrone 1992). This mechanism seems to be important in the release of protonemal gemmae, with a variety of different developmental patterns (Duckett & Ligrone 1992). Schnepf (1992) reported these from the chloronemata of *Funaria hygrometrica* (Figure 138), where they serve to fragment the protonemal filaments. In *Zygodon* (Figure 139-Figure 140), *Bryum pallens* (= *B. flaccidum*; Figure 141), and *Dicranoweisia cirrata* (Figure 142), they occur at the bases of axillary gemmae, and they are characteristic of foliar gemmae in *Calymperes* (Figure 143-Figure 144) (Duckett & Ligrone 1992).

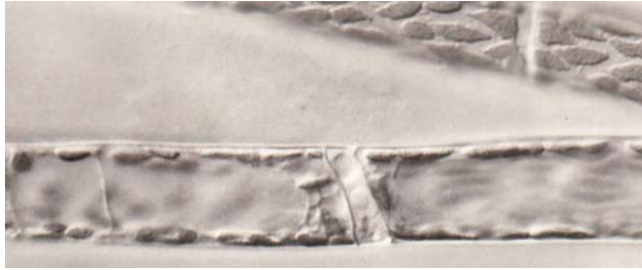


Figure 136. Protonema with short tmema cell where protonema can break apart. Photo by Jaime Goode, permission pending.

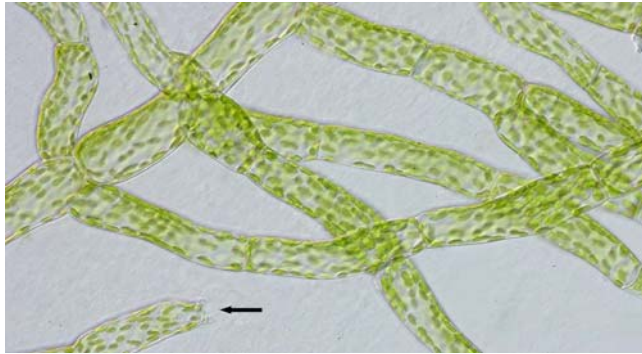


Figure 137. *Physcomitrella patens* protonema, showing broken cell that was a **tmema** (arrow). Photo by Anja Martin, Labor Ralf Reski <en.wikipedia.org/wiki/Ralf_Reski>, through Creative Commons.

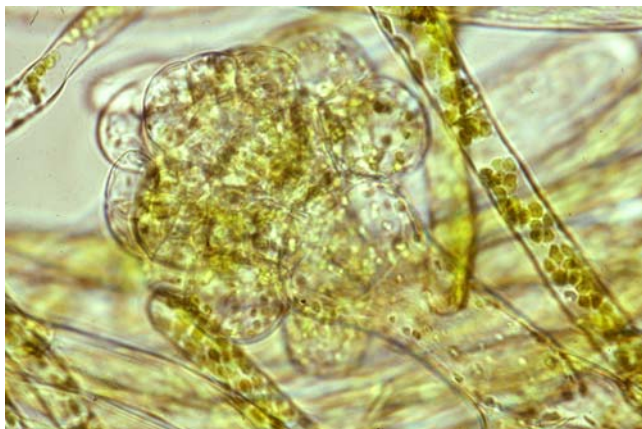


Figure 138. *Funaria hygrometrica* protonema with bud. Photo by Martin Bopp, with permission.



Figure 139. *Zygodon conoideus* growing on bark. Photo by Michael Lüth, with permission.



Figure 140. *Zygodon conoideus* gemmae. Photo by David Holyoak, with permission.



Figure 141. *Bryum pallens* (= *Bryum flaccidum*) with axillary filamentous gemmae attached by a tmema cell. Photo by Kristian Peters, with permission.



Figure 142. *Dicranoweisia cirrata* with capsules, a species that produces axillary gemmae with tmemata. Photo by Michael Lüth, with permission.



Figure 143. *Calymperes erosum* with leaf gemmae. Photo by Li Zhang, with permission.

The tmema cell in *Funaria hygrometrica* results from unequal cell division and is followed by the loosening of the old proximal cell wall (Bopp *et al.* 1991). Addition of 10 μ M IAA prevents the formation on tmemata, indicating that the formation of this cell results from inadequate IAA. The result of this fragmentation is to create several separate protonemata.



Figure 144. *Calymperes erosum* leaf with gemmae attached by tmemata. Photo by Li Zhang, with permission.

Diaspore Bank

Unfortunately, it is difficult to determine whether spores or asexual diaspores contribute to the growth of new plants from the diaspore bank. During (1995) suggested that tubers of some moss species may be very abundant in the diaspore bank, and as seen earlier in the discussion of diaspore banks, these species often are not represented above ground or are sparse there. During contends that such populations seem to rely completely on occasional recruitment. Long rhizoids help to extend the range of some species within a location. He considers population regulation of these species to be a density-dependent mortality of the tubers in the soil.

The forest is often disturbed, whether by fire or by harvesting. Bryophytes are important in maintaining soil moisture and as reservoirs of nutrients that often get released toward the later part of the growing season. Following disturbance, forest floor bryophytes are often recovered from diaspore banks. Caners *et al.* (2009) cultured mineral soil samples from both mixed and coniferous forest stands in northern Alberta, Canada, following harvesting. They found that forest type was not the determinant of the species composition, nor was harvesting intensity. Rather, edaphic variables and geographic space determined the regenerant flora. Nevertheless, light intensity exerted a significant influence on both the species responses and the species assemblages. Low light caused significant reduction in richness and cover of acrocarpous mosses – the fugitive, colonist, and shuttle life-history strategies. Pleurocarpous mosses (perennial stayers), on the other hand, seemed unaffected by light intensity. Higher light intensities supported significantly greater **Shannon diversity** and the frequency of reproduction. Caners *et al.* concluded that diaspore banks were an important repository for forest floor species and provided a source for recovery after harvesting.

Ross-Davis and Frego (2004) found 10 of the 36 species of a forest floor community in both the diaspore bank and the aerial diaspore rain. Of the extant taxa, 36% were not present in either diaspore source. The two dominant mosses, *Pleurozium schreberi* and *Hylocomium splendens*, were present in both the diaspore bank and aerial diaspore rain.

Hence, bryophytes are able to colonize disturbed areas from both the diaspore bank and from the diaspore rain. These two sources contain both spores and vegetative propagules, but not necessarily both from the same species. Distinguishing which type of diaspore germinated is quite difficult and is not usually included in diaspore bank studies.

The Antarctic undoubtedly has many well-preserved bryophyte diaspores buried in the ice and deep in bryophyte mats. Bergstrom and Selkirk (1999) were able to culture propagules from substrate samples 5.5 cm deep on Macquarie Island. They succeeded in germinating 15 bryophyte taxa. They hypothesized that bryophytes that arrived on bare patches in the feldmark, they were able to colonize stable ground but unable to colonize areas subject to surface movement. Instead, some of these propagules became buried. Spherical moss balls, however, were tolerant of the surface movement and disturbance. Of the 15 species that germinated, 10 were not local and came from populations at the warmer lower altitudes. They

suggested that such propagules will permit areas respond quickly to climate change by providing species that were tolerant to the new climate.

Propagule Dispersal Distances

It appears that little is known about actual distances that vegetative propagules might travel. Although studies have suggested that the distances are short, *i.e.* measured in centimeters rather than meters (Kimmerer 1991, 1994; Kimmerer & Young 1995), it appears that extensive measurements are lacking. Kimmerer (1991) found that gemmae of *Tetraphis pellucida* (Figure 18-Figure 19) travelled to a maximum of 10 cm in her study, and that 50% fell within 1 cm. But surely moss balls (see subchapter on growth forms) can travel great distances. And fragments of bryophytes on glaciers likewise travel hundreds of feet, and potentially much more. In my study on *Fontinalis* (Figure 145) vegetative dispersal, one piece had re-established upstream about 20 m from its origin, presumably carried there by some animal (bear or human?).



Figure 145. *Fontinalis antipyretica*, a moss that spreads vegetatively by rhizomes and disperses by fragments. Photo by Andrew Spink, with permission.

Convincing evidence of long-distance propagule dispersal is that of *Marchantia polymorpha* (Figure 146) on the crater of Deception Island, Antarctica. The crater was formed in 1969, exposing new ground following the eruption. In 1971, Young and Kläy reported this species on the new ground approximately 1000 km from the nearest known population in South America. No other colonies on Deception Island of this conspicuous liverwort were known to the scientists. Perhaps more surprising, the thallus had the distinctive dumbbell shape that is typical of a young thallus developed from a gemma! This example supports a conclusion of rapid long-distance dispersal that in this case arrived at a suitable habitat. (Let's hope this wasn't a case of inadvertent human dispersal!)



Figure 146. *Marchantia polymorpha* with gemma cups. Photo by Andrew Spink, with permission.

Propagule Survival/Longevity

The first question that comes to mind for long-distance dispersal of vegetative propagules is whether they can survive. These are living, often active fragments, gemmae, bulbils, and other structures that may or may not be dormant. Presumably, living fragments would be the least adapted among these to survive the conditions of the stratosphere. Studlar *et al.* (2007) tested fragment survivability by sending four mosses into the stratosphere on a weather balloon. These were subjected to temperatures as low as -30°C over a period of 4 hours, 2 of which were in the stratosphere. Subsequent culture for 28 days in the lab revealed the ability of these species to survive the stratosphere ride. *Sphagnum magellanicum* (Figure 147), *S. fallax* (Figure 148), and *Atrichum angustatum* (Figure 44) all regenerated with secondary protonemata and juvenile shoots. *Sphagnum girgensohnii* (Figure 149), however, did not. These results suggest that at least some vegetative diaspores, including fragments, could travel by wind into the stratosphere.



Figure 147. *Sphagnum magellanicum* in Europe, a species that survived travel in a weather balloon. Photo by Michael Lüth, with permission.



Figure 148. *Sphagnum fallax*, a species that survived travel in a weather balloon. Photo by Michael Lüth, with permission.



Figure 149. *Sphagnum girgensohnii* at Lake Perrault, MI, USA, a species that did not survive travel in a weather balloon. Photo by Janice Glime

Some bryophytes may survive in a dry state for years, providing a larger set of opportunities for the wind or water to distribute them to new locations. Whitehouse (1984) reported that tubers of *Anisothecium* (= *Dicranella*) *staphylinum* (Figure 150) survived in stored soil for 50 years. Zander (1979) successfully cultured *Anoetangium* (Figure 151), *Barbula* (Figure 152), *Desmatodon* s.l. (Figure 153), *Didymodon* (Figure 154), *Gymnostomum* (Figure 155), *Hymenostylium* (Figure 156), *Leptodontium* (Figure 157), *Molendoa* (Figure 158), *Oxystegus* (Figure 159), *Pleurochaete* (Figure 160), *Pseudocrossidium* (Figure 161), *Tortella* (Figure 162), *Tortula* (Figure 163), and *Trichostomum* (Figure 164) species, all members of **Pottiaceae**, from herbarium plants (not spore) specimens. These were all less than 5 years old.



Figure 150. *Dicranella staphylinina* on soil, a species that can survive storage in soil for 50 years. Photo by Michael Lüth, with permission.



Figure 151. *Anoetangium aestivum* with capsules, a species cultured from herbarium specimens less than 5 years old. Photo by Jan-Peter Frahm, with permission.



Figure 152. *Barbula unguiculata* with water on setae and capsules. This species was cultured from herbarium specimens less than 5 years old. Photo by Adnan Erdag, with permission.



Figure 153. *Tortula hoppeana* (syn.=*Desmatodon latifolius*) from the mountains in southern Europe. This species was cultured from herbarium specimens less than 5 years old. Photo by Michael Lüth, with permission.



Figure 154. *Didymodon rigidulus* in southern Europe, a species cultured from herbarium specimens less than 5 years old. Photo by Michael Lüth, with permission.



Figure 157. *Leptodontium flexifolium* in Europe, a species cultured from herbarium specimens less than 5 years old. Photo by Michael Lüth, with permission.



Figure 155. *Gymnostomum aeruginosum* with capsules in Europe, a species cultured from herbarium specimens less than 5 years old. Photo by Michael Lüth, with permission.



Figure 158. *Molendoa hornsuschiana* in southern Europe, a species cultured from herbarium specimens less than 5 years old. Photo by Michael Lüth, with permission.



Figure 156. *Hymenostylium recurvirostrum* in India, a species cultured from herbarium specimens less than 5 years old. Photo by Michael Lüth, with permission.



Figure 159. *Oxystegus cylindricus* subsp. *hibernicus*, a species cultured from herbarium specimens less than 5 years old. Photo by Jan-Peter Frahm, with permission.



Figure 160. *Pleurochaete squarrosa* wet, a species cultured from herbarium specimens less than 5 years old. Photo by David T. Holyoak, with permission.



Figure 161. *Pseudocrossidium revolutum*, a species cultured from herbarium specimens less than 5 years old. Photo by Proyecto Musgo, through Creative Commons.



Figure 162. *Tortella flavovirens* in southern Europe. Photo by Michael Lüth, with permission.



Figure 163. *Tortula muralis* with water drops in Dunblane, Scotland. This species was cultured from herbarium specimens less than 5 years old. Photo courtesy of Peggy Edwards.



Figure 164. *Trichostomum brachydontium*, a species cultured from herbarium specimens less than 5 years old. Photo by Barry Stewart, with permission.

Buried propagules must somehow remain dormant in an environment (diaspore bank) that varies both their temperature and their state of hydration. The only factor they lack for germination appears to be light. Risse (1987) reviewed 82 species of European mosses with rhizoidal propagules and demonstrated that tubers and rhizoidal gemmae do not germinate in absence of light. Their germination is dependent upon the intensity of light, not the photoperiod. If the propagules are hydrated for more than ten days without successful germination they do not survive. After fifteen days, their fat reserves are depleted. Furthermore, imbibition of water causes the gemmae to lose their dormancy and become sensitive to dehydration, causing irreversible damage if they are more than 12 hours into their pre-germination phase when they dry out again. This can explain the absence of viable propagules in the first cm of soil where frequent wetting and drying are certain.

Egunyomi (1978) found that spores have longer storage longevity than do gemmae for *Octoblepharum albidum* (Figure 13). Even at room temperature and 60-75% humidity, spores were viable after eight months, but gemmae began to lose viability at six months. Light is of utmost importance for germination, with only 8.0% of gemmae germinating at 1 lux, but 90% at 1375 lux.

Imura and coworkers (1992) experimented with the rhizoidal tubers of a moss, *Leptobryum pyriforme* (Figure 165-Figure 170), found on the ice surface of a lake near the Syowa Station in the Antarctic. Both protonemata and

leafy shoots developed from these tubers after the tubers had been stored for two years in a freezer. This illustrates the tremendous tolerance of these species and the extraordinary survival abilities.



Figure 165. *Leptobryum pyriforme* with capsules, a species with tubers that can survive two years in a freezer. Photo by Michael Lüth, with permission.



Figure 166. *Leptobryum pyriforme* with tubers from wet meadow and stagnant ditch Minnesota, USA. Photo by Jan Janssens, with permission.



Figure 167. *Leptobryum pyriforme* rhizoidal tuber. Photo by Victoria Rozhina.

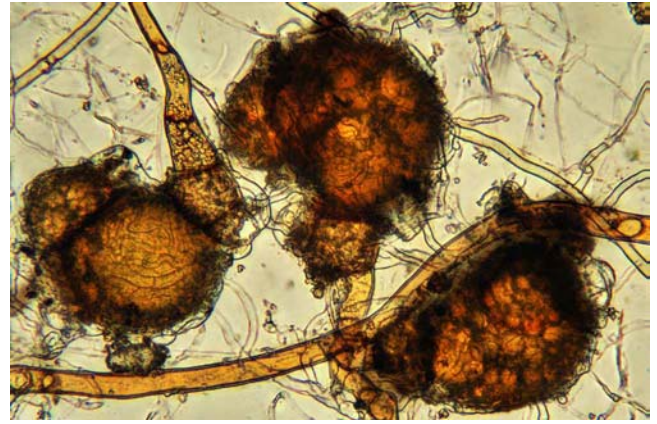


Figure 168. *Leptobryum pyriforme* rhizoidal tubers. Photo by Dick Haaksma, with permission.

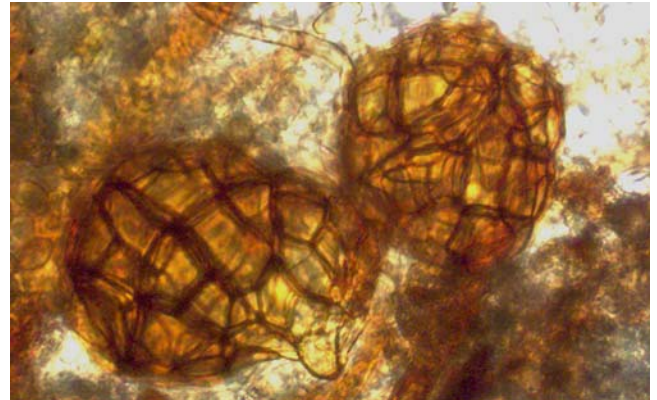


Figure 169. *Leptobryum pyriforme* rhizoidal tubers. Photo by Victoria Rozhina.

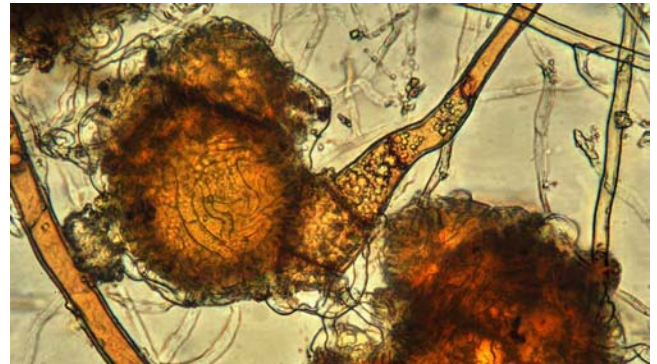


Figure 170. *Leptobryum pyriforme* rhizoidal tubers. Photo by Dick Haaksma, with permission.

John Spence (Bryonet 22 November 2010) actually tested long-term viability of tubers in *Rosulabryum capillare* (Figure 171) and *Gemmabryum* (= *Erythrocarpa* sp.; Figure 172). Tubers of these species remained viable up to 15 years and germinated in distilled water and normal daylight. Such propagules can remain dormant in soil banks and other locations, germinating after unknown periods of time when they are disturbed and brought to the surface (e.g. During 1999). Although there are a number of studies on propagules from such situations, the longevity of these propagules is unknown. Herbarium specimens provide a means of checking longevity, but the conditions of a herbarium are quite different from the natural habitat. And even if the propagules could survive the conditions there, they may become dinner for hungry invertebrates.



Figure 171. *Rosulabryum capillare* with capsules, a species whose rhizoidal gemmae can survive at least 15 years. Photo by Tom Thekathyl, with permission.



Figure 172. *Gemmabryum dichotomum* with bulbils. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Mishler and Newton (1988) experimented with four *Tortula* s.l. species (Figure 91-Figure 92; Figure 117-Figure 119) and found that fragments, while being less successful at germination than spores, usually developed numerous stems, whereas the spores did not during the 2.5 months of experiments. The protonemata looked different between the spore-derived and the fragment-derived ones. Perhaps they differed physiologically and those derived from spores required a day length or other condition not present in the experiment.

I have observed diatom-covered mosses being eaten by a dipteran larva in the *Rhyphidae* family. These went in "dirty" and came out the other end clean and still bright green. But I have no evidence that these actually survived the digestive tract as viable propagules. Insect guts can have extremely high or extremely low pH (Nation 2002) to adapt them to digestion of the few remaining nutrients in detritus, and the particular diet of this larva suggests it might be so-adapted. These extreme pH levels are likely to be detrimental to the living cells of the moss.

The potential of a delayed response of the moss to such a detrimental gut environment is exemplified by our experiment on *Fontinalis duriaei* (Figure 173). In an experiment to determine if rainbow trout (*Oncorhynchus mykiss*) could be dispersal agents of *F. duriaei*, we brought in fresh moss with lots of aquatic insects, but the fish did not eat the moss, so we force-fed it. The moss was expelled later through the anus in a neat cylindrical package (Figure 174), still bright green. We isolated it in a cooled jar of its own stream water, but 24 hours later, the moss had lost its green color and appeared to be dead.

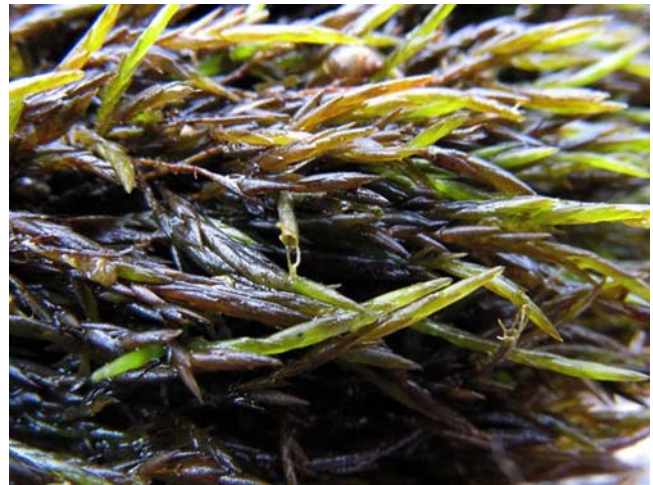


Figure 173. *Fontinalis duriaei*. Photo by Jan-Peter Frahm, with permission.



Figure 174. Feces packet from rainbow trout, containing *Fontinalis duriaei* that has lost its green color 24 hours after its egestion. Photo by Janice Glime.

Vegetative propagula are less likely to survive travel through the gut than spores, and they may be more susceptible to damage when they begin to germinate as well. Hydration without successful germination can kill them. But if they are able to germinate successfully, both fragments and specialized propagula have better chances than spores of producing gametophores, albeit only one per propagule. Propagule banks typically reflect not only the present vegetation, but also past vegetation, providing ready sources following disturbance.

One prerequisite for propagules with long dormancy or lengthy travel is desiccation tolerance. Understanding this

is necessary for cryopreservation to maintain species that may become extirpated in the future. Rowntree *et al.* (2007) have used cryopreservation successfully for many species and in doing so have added greatly to our understanding of the mechanisms the bryophytes are able to use to survive. They have found that survival can be enhanced by pretreatment with ABA and sucrose, the latter perhaps providing an energy source upon rehydration. Surprisingly, the pioneer moss *Ditrichum plumbicola* had low survival of cryopreservation and likewise responded poorly to pretreatment. With further experimentation, they discovered that the pretreatment with sucrose and ABA caused significant changes in the protonemata. Growth was greatly reduced and propagules had pronounced morphological and cytological changes. Although most cells died, those that survived were markedly different from normal. The surviving cells had thick walls that were darkly pigmented and there were numerous small vacuoles and lipid droplets in the cytoplasm. When there was no ABA-sucrose pretreatment, desiccation and cryopreservation caused minimal cytological changes. These untreated tissues returned to their pre-dehydration state within 2 hours of rehydration. On the other hand, rehydration was normal once ABA and sucrose were removed from the pretreated propagules. Rather, these propagules (from the protonemata) became highly desiccation and cryopreservation tolerant, a behavior similar to that of rhizoids that function as perennating organs in the field. Rowntree and coworkers considered this as evidence that the propagules used ABA to increase their desiccation tolerance.

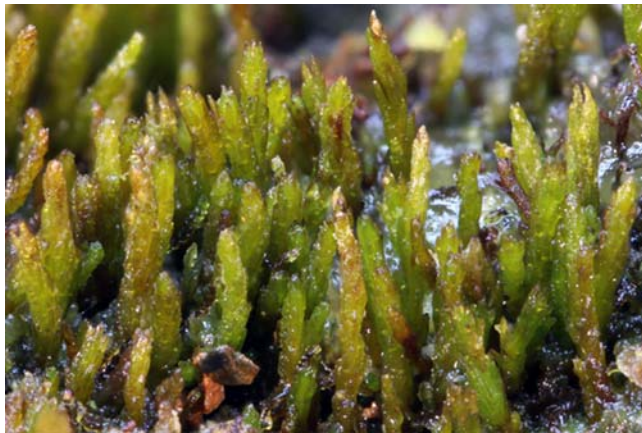


Figure 175. *Ditrichum plumbicola*, a species with low cryopreservation survival. Photo by Des Callaghan, with permission.

In *Marchantia inflexa* (Figure 176) both water and desiccation affect mortality (Chris Stieha, Bryonet 27 February 2016). In his lab, there was less than 10% mortality of gemmae maintained in water for three months, but 20% mortality after only four days of desiccation. In the field they can turn brown within an hour of desiccation. Stieha *et al.* (2014) found that male plants of this species produce the most gemmae and more quickly when compared to females, but the male gemmae have less ability to survive desiccation. Gemmae in this species can move up to 20 cm from the parent plant in a light rain, permitting expansion of the population.



Figure 176. *Marchantia inflexa*, a species whose gemmae survive well in water but tolerate little desiccation. Photo by Scott Zona, with permission.

Propagule Establishment

Once a propagule reaches its final resting place, it must begin growth and become established (Figure 177). Due to both edaphic and climatic differences, the success of this establishment is less predictable as the distance increases (Karlson & Taylor 1992; Ronsheim 1997; Laaka-Lindberg *et al.* 2003).

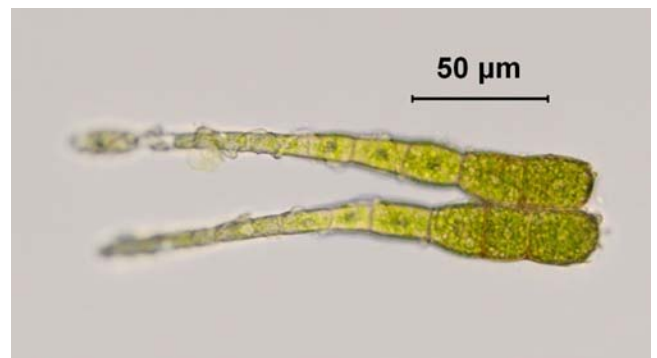


Figure 177. Gemmae germinating. Photo by Li Zhang, with permission.

The conditions at germination can be critical. Risse (1987) tested rhizoidal gemmae of mosses, citing their importance in environments that are frequently disturbed by natural or anthropogenic influences. McCutcheon (1978) reported that light is required for germination, and that if the gemma of *Bryum rubens* (Figure 178-Figure 181) becomes imbibed for more than ten days without receiving light, it will die. Its fat storage reserves are depleted in 15 days, so that imbibition can trigger that loss. Furthermore, after imbibition, tubers become sensitive to desiccation and do not regain their pre-germination tolerance if they have entered their pre-germination phase (imbibed) for more than 12 hours.

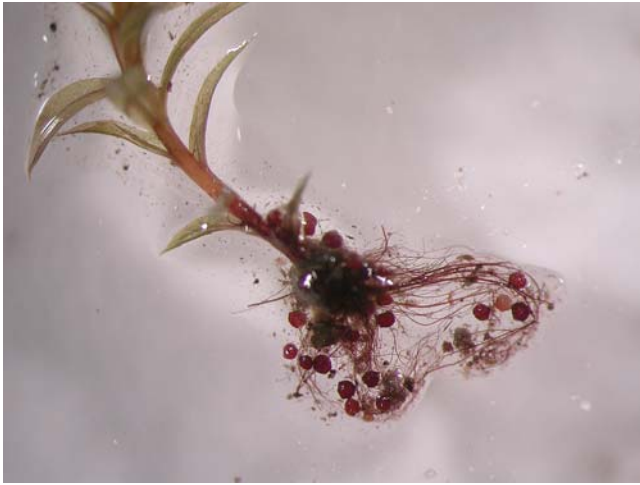


Figure 178. *Bryum rubens* rhizoidal gemmae. Photo by Ariel Bergamini, with permission.



Figure 179. *Bryum rubens* rhizoidal gemmae along stem rhizoids. Photo by Ariel Bergamini, with permission.

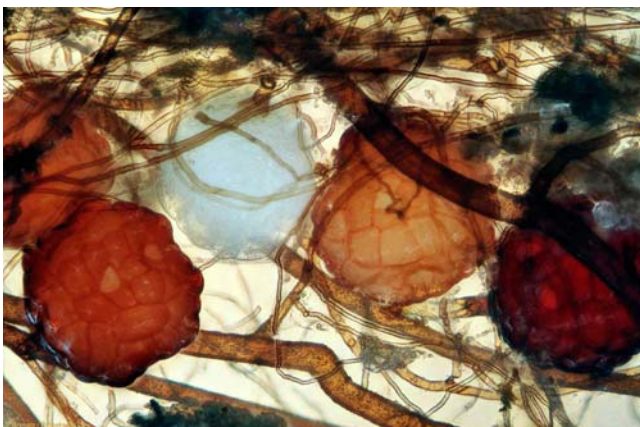


Figure 180. *Bryum rubens* rhizoidal tubers in various stages of maturity, showing how prolific they can be. Photo by Dick Haaksma, with permission.

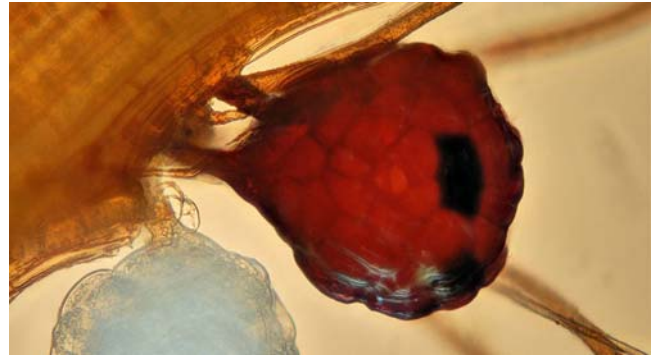


Figure 181. *Bryum rubens* rhizoidal tubers. Photo by Dick Haaksma, with permission.

Desiccation

A key factor in establishment is maintenance of sufficient moisture in early stages of development to permit development of a reproductive adult. An interesting example of this is *Pseudoscleropodium purum* (Figure 182). One habitat where this species grows is on ant hills of the yellow meadow ant, *Lasius flavus* (Figure 183), that is, on the north-facing sides of the ant hills (King 2003). Fragments detached by grazing animals are common on the mounds. After experimentation, King concluded that inability to establish on the south-facing side was most likely due to desiccation and metabolic drain leading to cell death. Transplanted adult mosses, on the other hand, seemed capable of survival.



Figure 182. *Pseudoscleropodium purum*. Photo by Michael Lüth, with permission.



Figure 183. The yellow meadow ant, *Lasius flavus*. Photo through Creative Commons.

Inhibitors

Gemmae do have a safeguard against competing with their parents. Most are inhibited by the presence of the parent (Figure 184) and are often even inhibited by related species [e.g. *Bryum rubens* (Figure 178-Figure 181) by *Bryum alpinum* (Figure 185) (McCrutcheon 1978)]. Ashton and Raju (2001) demonstrated inhibition of rhizoidal gemmae in *Gemmabryum* (= *Bryum*) *violaceum* (Figure 186) by the soil associated with the parents, but gemmae germinated while still attached if placed in fresh soil. This suggests that whatever served as the deterrent may have accumulated in the soil to a greater level than that in the plant. It would be interesting to attempt growing these in the same soil with charcoal as an adsorbant.



Figure 184. *Lunularia cruciata* showing ungerminated gemmae on thallus. Both *Marchantia* and *Lunularia* inhibit the germination of the gemmae on the parent. Photo by Martin Hutten, with permission.



Figure 185. *Bryum alpinum* showing competition. Photo by David T. Holyoak, with permission.

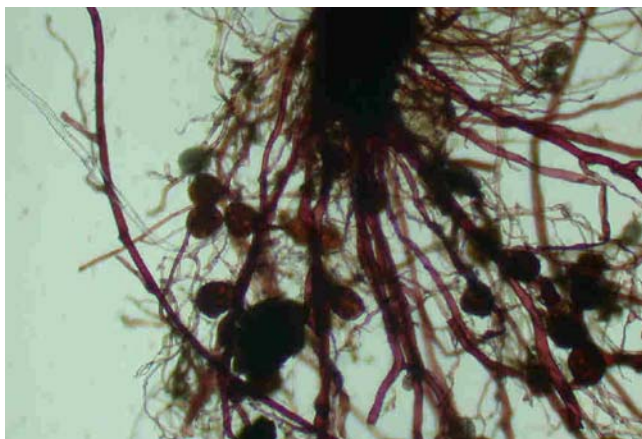


Figure 186. *Gemmabryum violaceum* with rhizoidal tubers. Photo by David T. Holyoak, with permission.

Risse (1987) suggested that this inhibition might be caused by sugars, particularly mono- and disaccharides, shown by McCrutcheon (1978) to inhibit tuber germination in *Bryum rubens* (Figure 178-Figure 181). Christianson (2000) showed that ABA (abscisic acid) is able to inhibit bud formation in *Funaria hygrometrica* (Figure 187), so it could also be the cause of inhibition by parents. This same self-inhibition (inhibition by parents) is known from *F. hygrometrica* (Figure 187). On the other hand, the cytokinin hormones leaked from one individual can stimulate bud formation on other nearby individuals of the same or related species (Bopp 1982).



Figure 187. *Funaria hygrometrica* showing the distinct margins where colonies contact each other. Photo by Janice Glime.

ABA is a common hormone in tracheophytes, having a variety of functions. It is best known in bryophytes as a responder to desiccation. Mallón *et al.* (2006) examined the effect of various concentrations of ABA on the production and behavior of gemmae in *Splachnum ampullaceum* (Figure 129). This species is best known for its ability to attract flies that disperse it among piles of dung, but its ability to produce vegetative propagules was previously unknown. The researchers managed to induce both brood cells and chloronemal bulbils in their protonemal cultures, as well as vegetative propagules, and their results suggest a bet-hedger strategy. The brood cells produced new chloronemal filaments when they were transferred to new media. There was a direct positive relationship between the concentration of ABA and brood cell formation, while at the same time increasingly inhibiting the growth of the protonemata. Furthermore, no buds developed on protonemata grown on media with ABA. Mallón and coworkers suggested that production of the vegetative structures on the protonema might be a desiccation response and would permit the plant to spread rapidly, a behavior that might also help to conserve moisture, if not then, in the future.

Establishment and Rarity

Cleavitt (2002) attempted to determine the factors that contributed to rarity of species [*Mielichhoferia macrocarpa* (Figure 188), *Didymodon johansenii*, and *Mnium arizonicum* (Figure 135)] and compared three rare

and common species pairs in the Front Ranges of Alberta, Canada. She found that propagule viability did not relate to establishment ability. Rather, establishment of rare species may be a function of a complexity of mechanisms that create a narrow realized niche. For example, *Mielichhoferia macrocarpa*, which occurred in the darkest and wettest sites, was tolerant of high light intensity and desiccation, suggesting that additional factors narrowed its establishment niche. She suggested that the broader apparent physiological tolerance found in these rare species may be due to their greater reliance on asexual reproduction. This suggests that we should look for other physiological factors and dispersal as causes of rarity.



Figure 188. *Mielichhoferia macrocarpa*, a species that appears to have broad environmental tolerances, but with limiting requirements of some factor(s). Photo by Robin Bovey, with permission through Dale Vitt.

In contrast, Cleavitt (2002) found that the three common species [*Mnium spinulosum* (Figure 189), *Bryum pseudotriquetrum* (Figure 190), *Didymodon rigidulus* (Figure 191)] were more likely to occupy habitats that agreed with their physiological requirements. *Mnium spinulosum* was limited by high light and thus occurred only in deeply shaded conifer stands; *Bryum pseudotriquetrum* was intolerant of desiccation and was thus found in moist areas such as stream banks.



Figure 189. *Mnium spinulosum*, a common species that is intolerant of high light and lives in conifer forests. Photo by Michael Lüth, with permission.



Figure 190. *Bryum pseudotriquetrum* at streamside. Photo by Michael Lüth, with permission.



Figure 191. *Didymodon rigidulus*, a common species. Photo by Michael Lüth, with permission.

Cleavitt (2002) suggests that rare species may have broader physiological tolerance because they rely on vegetative reproduction largely as fragments. In particular, they have a high tolerance to desiccation in both whole colonies and in fragments. This suggests that they may be rare due to dispersal limitations, slow establishment rates

that permit competitors to overpower them, or special environmental factors that were not examined.

Reproductive Problems

But the problems don't end with germination or even successful production of gametophores. These gametophores must likewise be able to reproduce, whether by vegetative means or spores. This is particularly problematic for dioicous species because they must have the successful invasion of both male and female spores for any further reproduction by spores to occur. And if they did arrive at a distant location by spores, it is likely that this is their primary means of dispersal. The same problem exists for vegetative propagules. For dioicous taxa, it is possible that only one gender arrives, whether by specialized structures or by fragments.

Perhaps there are species where the spores travel in tetrads, as is known for *Haplomitrium gibbsiae* (Figure 192) (Van Zanten & Pócs 1981). Nevertheless, a tetrad of spores is larger and hence sacrifices ease of transport by air currents. Van Zanten and Pócs suggest that this limitation might also be overcome by having spores remain in relatively compact clouds during transport – a notion that is certainly worthy of consideration. We need to consider if this compact cloud approach might also work for vegetative diaspores.



Figure 192. *Haplomitrium gibbsiae*, a species where spores travel in tetrads. Photo by Jan-Peter Frahm, with permission.

Epiphytes

It is hard enough to land in the right microhabitat on the ground, but even more challenging to land on a vertical surface. Hence, highly structured bark has more chance of trapping the somewhat large vegetative propagules. But the problems are just beginning at landing. The vertical surface of almost anything is subject to drying, and tree trunks are particularly exposed. Fortunately, the tropical cloud forests manage to maintain a higher moisture content than other types of forest habitats and thus are endowed with dense bryophyte cover on everything (Figure 193).

As one can imagine, establishment of tracheophytes can be more difficult than that of bryophytes. Hence, many depend on bryophyte establishment to provide them with a suitable substrate (Nadkarni *et al.* 2000). Nadkarni and co-workers dropped epiphytic bryophyte fragments 50 cm

above branches of saplings and mature trees of *Ocotea tonduzii*. Only 1% of these fragments were returned for the six months of the experiment. During the same time period, branches in the canopy with intact epiphyte loads retained 24% and branches that had been stripped of their epiphytes retained 5%. They found that a larger surface area and presence of other bryophytes helped in the retention of the fragments.



Figure 193. Mossy forest, Malaysia, where high moisture levels make it easy for epiphytic bryophytes to establish. Photo by Vita Plášek, with permission.

Rosso *et al.* (2001) found that *Antitrichia curtispindula* (Figure 194-Figure 195) grows faster in the canopy (60% faster) than in the understory, making it easier for it to become established there than when it falls on lower branches. These researchers considered that its absence in young stands may be due to dispersal limitations compared to that in old growth stands. In old growth stands it has both greater height to launch dispersal and more time to get there.



Figure 194. Habitat of the epiphytic *Antitrichia curtipendula*. Photo by James K. Lindsey, with permission.



Figure 195. *Antitrichia curtipendula* on a branch. Photo by James K. Lindsey, with permission.

Symbionts Needed

For some bryophytes, a symbiotic relationship is important to survival. *Blasia pusilla* (Figure 196) and *Cavicularia densa* (Figure 197) have solved this problem by producing gemmae that include their *Nostoc* symbiont (Figure 198) (Rikkinen & Virtanen (2008). Others benefit from the presence of soil Cyanobacteria such as *Anabaena variabilis* and *Nostoc muscorum*, as is the case for *Funaria hygrometrica* (Rodgers & Henriksson 1976). These Cyanobacteria are able to capture atmospheric nitrogen and make it usable for the bryophytes.

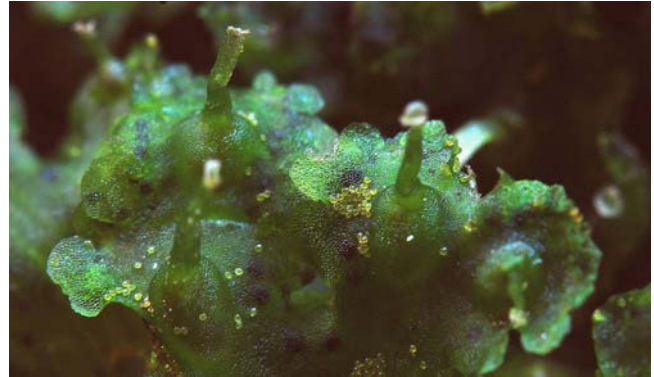


Figure 196. *Blasia pusilla* with *Nostoc* colonies (dark blue). Photo by Dick Haaksma, with permission.



Figure 197. *Cavicularia densa* with gemmae and *Nostoc* colonies. Photo from Digital Museum Hiroshima University, with permission.

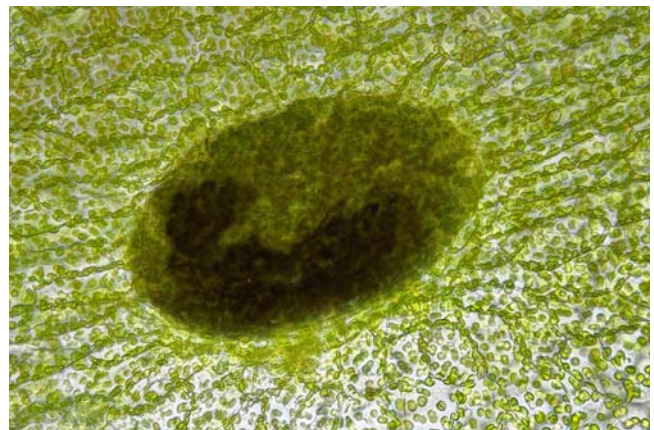


Figure 198. *Nostoc* colony on *Blasia pusilla* thallus. Photo by Dick Haaksma, with permission.

Other bryophytes need fungal partners (Figure 199) (Bidartondo *et al.* 2003; Martinez-Abaigar 2005; Bidartondo & Duckett 2010; Pressel *et al.* 2010; Bidartondo *et al.* 2011; Desirò *et al.* 2013). Although there

have been a number of studies on fungi associated with various bryophytes, these have not dealt with the need for partners at the time of establishment of vegetative diaspores. Are vegetative dispersal structures able to carry their partners with them? Even if so, the conditions must be right for such a partner to flourish along with the bryophyte.

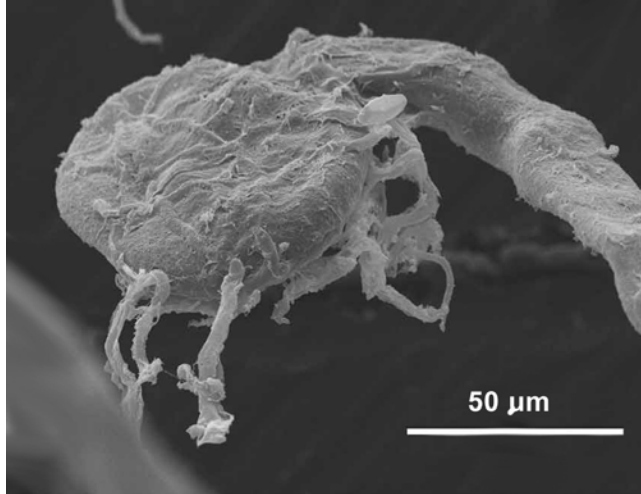


Figure 199. *Mylia anomala* rhizoid tip with symbiotic Ascomycete. Photo courtesy of Silvia Pressel, Robert Ligrone, and Jeffrey Duckett.

A somewhat similar problem occurs for *Dicranum flagellare* (Figure 23) on logs. It seems to be dispersal limited and can only colonize gaps caused by disturbance when other populations occur nearby (Kimmerer 1994). Therefore, older forests where there are more colonized logs provide a better source of propagules for dispersal. But once it reaches a substrate, it germinates much more rapidly than *Tetraphis pellucida* (Figure 18-Figure 19) and persists there longer, perhaps through competition.

Bacteria are important for the development of some bryophytes from spores (Spiess *et al.* 1984), so it is likely that these are also needed for some propagules to complete development, particularly those forming protonemata first.

Tradeoffs

Size matters in dispersal of propagules, but it invokes a tradeoff. Small propagules have the advantage of being produced in large numbers, *e.g.* 500-700 gemmae per leaf in *Scapania nemorea* (Figure 98-Figure 102) with 1-celled gemmae or 1000-7000 1-celled gemmae in *Lophozia ventricosa* var. *silvicola* (Figure 103) compared to only 15-45 in *Jubula* (= *Radula*) *complanata* (Figure 104-Figure 105) with discoid, multicellular gemmae (Laaka-Lindberg *et al.* 2003). Larger gemmae, on the other hand, have a greater chance for successful establishment where they arrive due to more stored energy.

It is also possible that the vegetative tissues of the vegetative diaspores may provide greater protection against germination in the wrong environment. Spores need only light and water to germinate. Hence, when they are brought to the surface and get a good rain, they germinate. As far as we understand, they do not, as spores, detect whether any other aspect of the environment is suitable. Some vegetative propagules, on the other hand, may be

able to detect inappropriate conditions of pH, insufficient nutrients, absence of a fungal partner, absence of hormones from associated bacteria, inappropriate temperature, or toxic metals and other substances. Examining these possible controls on germination of vegetative propagules may help us to understand both longevity of diaspores in the diaspore bank and the comparative success of spores vs vegetative diaspores.

Summary

Vegetative reproduction includes fragments, gemmae, and vegetative diaspores. A genet is therefore those individuals that arise from a single zygote, parthenogenetic gamete, or spore and that produce branches vegetatively. There are six basic means of reproducing vegetatively: 1) multiple gametophores from the protonema of one spore, 2) decay of older gametophyte parts with the separation of younger parts, 3) development of multiple shoots by rhizomes and stolons, 4) development of gametophores from rhizoids, 5) regeneration from fragments, 6) production of specialized propagula. The success of vegetative propagation is due to selection in the face of the difficulty of accomplishing sexual reproduction in a terrestrial environment. Fragmentation is especially common among pleurocarpous, perennial mosses where the dioicous condition and small spore size reduce the success of sexual reproduction. Such fragments can reach densities of 4000 viable propagules per cubic meter of snow. Propagula differ from gemmae in having an apical cell that can grow directly into a leafy shoot without a protonema stage. Propagula include deciduous shoot apices, caducous branchlets, flagella, and bulbils. Rhizoidal tubers can occur underground and many kinds of protonemata produce gemmae.

Splash cups are useful in dispersing gemmae in several liverworts and one family of mosses. Bryophytes getting frozen in ice or caught by flood waters can be carried considerable distances and vegetative dispersal in flowing water environs is essentially guaranteed. But vegetative diaspores have few mechanisms that aid in their liberation and dispersal. Among these are **tmema**, small cells that form a weak link and permit breakage.

Propagules must survive the desiccation, temperatures, and UV light of travel, be able to remain dormant upon arrival until the habitat or weather is suitable for germination, then survive after germination for the dispersal to be successful. Some have inhibitors such as ABA. Some require bacteria or fungi as partners. Some must land and become attached to vertical substrates. The usually larger vegetative structures sacrifice long distance dispersal for the ability to carry more with them and become established more easily. In addition to ABA, sucrose may also help in the survival of desiccation.

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CHAPTER 4-11

ADAPTIVE STRATEGIES: VEGETATIVE DISPERSAL VECTORS

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CHAPTER 4-11

ADAPTIVE STRATEGIES: VEGETATIVE DISPERSAL VECTORS



Figure 1. *Pohlia annotina* with bulbils in leaf axils. Many species survive on dispersal of vegetative propagules. Photo by Dick Haaksma, with permission.

Dispersal

Laaka-Lindberg *et al.* (2003) stated that dispersal pattern of vegetative propagules (*e.g.* Figure 1) is affected both by the microtopography of the habitat (Kimmerer & Young 1996) and by the type and size of propagule (Söderström & Herben 1997). Kimmerer (1994) further demonstrated that two log-dwelling species [*Orthodicranum flagellare* (Figure 2) and *Tetraphis pellucida* (Figure 33)] differed in the dispersal ability of their propagules.

Conditions upon arrival can play a role in which species can become established following dispersal. Gradstein (2006) demonstrated this with the lowland cloud forest of French Guiana. Vegetative propagules there are protected from desiccation by the daytime fog, permitting good photosynthesis despite high temperatures. Asexual reproduction is significantly more common in the understory than in the canopy despite the greater

constraints on dispersability in the understory. The canopy seems to experience better dispersal by spores.



Figure 2. *Orthodicranum flagellare* with broken brood branches lying on top of the cushion. Most likely some of these have travelled with an animal that broke them off. Photo by Janice Glime.

Gravity

Whereas spores are light weight and therefore easily lofted away on a slight air current, vegetative structures are often much more bulky and heavy. Shed parts, unless caught in a gust that can even blow heavy maple fruits up into the air, are likely simply to fall to the ground. This seems to be a common means for structures like gemmae, deciduous perianths, and other bulky forms of brood bodies and fragments.

"Galloping mosses" have an intriguing movement, leaving behind a trail of changed rock (Figure 3). The actual method of movement and time required is unknown, but they seem to move rather slowly, staying long enough in one place to chemically change the surface of the rock. Hence, it appears that gravity plays at least a partial role, but water most likely also helps in the movement. Mosquin (2011) reported these slowly moving mosses from the Arctic, where the mosses *Sphagnum* and *Grimmia ovalis* (Figure 3), and *Racomitrium ericoides* (Figure 4) are known for this behavior. When they reach a crack, they may be stopped and remain there (Figure 5).



Figure 3. *Grimmia ovalis* "galloping." Photo by Wouter Bleeker, with permission.

Wind Dispersal

Imagine being a small fragment of a leaf or stem being blown by the wind. Lacking the protection of surrounding plants, desiccation is imminent. Bouncing on the ground or off trees or rocks could impose a significant blow to tissues that may be only one cell thick. Exposure to UV radiation is likely to be greater than in their normal niche. Nevertheless, using a weather balloon Studlar *et al.* (2007) showed that at least some species [*Sphagnum fallax* (Figure 6), *S. magellanicum* (Figure 7), *Atrichum angustatum* (Figure 8)] can survive these conditions and regenerate from fragments.



Figure 4. *Racomitrium ericoides*, a moss that contributes to galloping mosses. Photo by Janice Glime



Figure 5. *Grimmia ovalis* trapped by cracks, with two clumps that managed to break loose, perhaps because of their larger size. Photo by Wouter Bleeker, with permission.



Figure 6. *Sphagnum fallax*, a species that seems capable of surviving wind dispersal. Photo by Michael Lüth, with permission.



Figure 7. *Sphagnum magellanicum*, a species that can regenerate from windborne leaf fragments. Photo by Michael Lüth, with permission.



Figure 8. *Atrichum angustatum*, a species that regenerates from leaf fragments. Photo by Bob Klips, with permission.

This demonstration gives credence to a number of studies that have inferred vegetative dispersal of bryophytes. And we have already seen viability in 12% of the fragments blown about on the snow in Canada by wind (Miller & Howe Ambrose 1976).

In the Antarctic, Skotnicki *et al.* (2000) found evidence of propagule dispersal from elsewhere, with the RAPD technique indicating short-distance dispersal by both wind and water and long-distance dispersal by wind across the ice caps. The genetic similarities of *Chorisodontium aciphyllum* (as *Sarconeurum glaciale*; Figure 9) from three locations on Ross Island, Antarctica, with those of Arrival Heights, Scott Base, and Crater Hill, a few km away suggest wind dispersal, a concept supported by the prevailing wind direction and absence of the species in areas in between.

Water Dispersal

Water aids in the dispersal of bryophytes in multiple ways. Aquatic mosses most likely depend primarily on water dispersal. Sexual organs can easily be damaged by abrasives in the water, as for example those in *Platyhypnidium riparioides* (Figure 10; Lewis 1973). These same abrasives can free leaves and branches that are possibly able to lodge on a substrate and regenerate.

Conboy and Glime (1971) found similar abrasion in stream populations of *Fontinalis novae-angliae* (Figure 11).



Figure 9. *Chorisodontium aciphyllum*, an Antarctic moss that is apparently dispersed by both wind and water. Photo by Jan-Peter Frahm, with permission.



Figure 10. *Platyhypnidium riparioides* in Europe, showing darkened and scoured leaves on lower parts of stems. Photo by Michael Lüth, with permission.



Figure 11. *Fontinalis novae-angliae* scoured by stream flow and suspended particles. Photo by Janice Glime.

Fontinalis species in streams are faced first with the problem of producing few sporophytes (Sayre 1945; pers. obs.), then of having spores lodge in a suitable place to stay put and begin new growth, whereas branches can easily get caught against rocks or snagged by submerged branches and roots, giving them an opportunity for new establishment (Figure 12; Sayre 1945; Welch 1948; Glime *et al.* 1979). Once these fragments get lodged against a rock or other suitable substrate, the contact stimulates the growth of rhizoids that eventually attach them to the substrate (Welch 1948; Glime *et al.* 1979; Figure 13-Figure 14). But this takes time, and experiments indicate that it requires at least nine weeks of impingement before the actual attachment (Figure 15; Glime *et al.* 1979). Temperature and flow rate influence the development of these rhizoids in *Fontinalis duriaei* (Figure 16) and *Hygroamblystegium fluviatile* (Figure 17), with flowing water conditions causing the mosses to produce more rhizoids than pool conditions (Glime 1980).



Figure 12. *Fontinalis novae-angliae* becoming established from a rhizome fragment in Fox Run, Grafton County, NH, USA. Photo by Janice Glime.



Figure 13. Rhizoids developing from stem wound tissue of *Fontinalis squamosa*. Note the spiral growth. These have not yet contacted a substrate. Photo by Janice Glime.

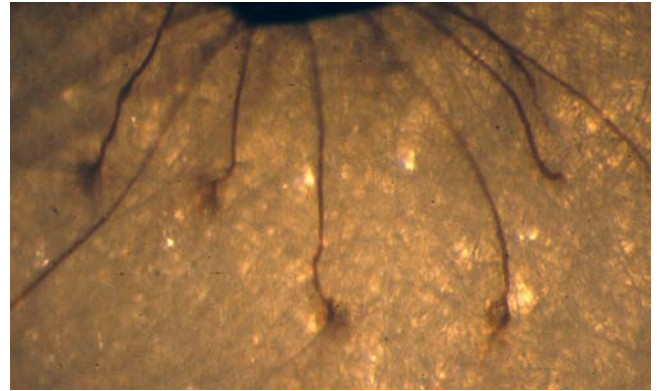


Figure 14. Rhizoids from wounded stem tissue of *Fontinalis squamosa*, showing the branched growth at their tips where they have contacted a substrate. In this case, the substrate is filter paper in contact with a glass test tube. Photo by Janice Glime.

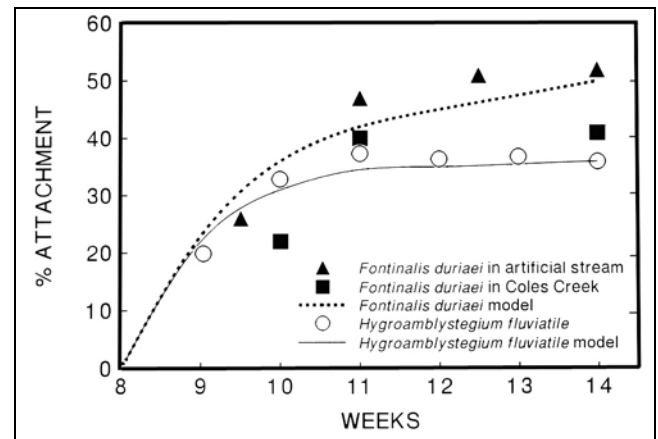


Figure 15. Comparison of times required and percentage of attachment for *Fontinalis duriaei* and *Hygroamblystegium fluviatile* in contact with rocks in an artificial stream (n=48) compared to rocks placed in Coles Creek, MI, with *F. duriaei* held in contact with netting. Based on Glime *et al.* 1979.

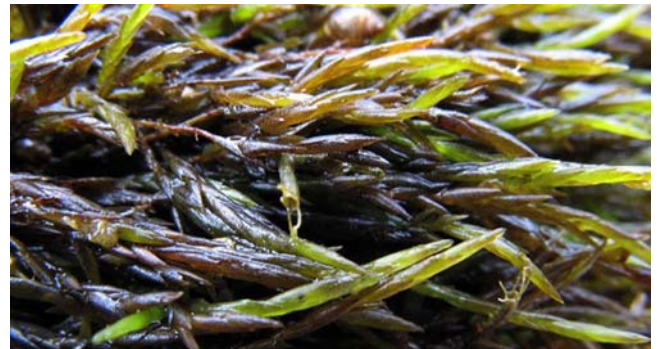


Figure 16. *Fontinalis duriaei* in Europe. Photo by Jan-Peter Frahm, with permission.



Figure 17. *Hygroamblystegium fluviatile* fragment in culture, showing dense rhizoids that formed, possibly in response to the substrate. Photo by Janice Glime.

In these early experiments, the moss fragments were held against the rocks with netting (Glime *et al.* 1979). But the field application of this concept was then tested by tagging 750 stems of *Fontinalis duriaei* (Figure 16) growing in Big Valley Creek, a forested stream in the Keweenaw Peninsula, Michigan, USA (Glime *et al.* 1979). Within the two years following tagging, many mosses could not be found again. But the proof of dispersal lies in two tagged mosses that were found in a different location. One of these was relocated downstream 60 weeks after the tagging date. The second was found nearly 100 m upstream! Possible upstream dispersal agents were fishermen and the black bear (*Ursus americanus*; Figure 18) that chased my graduate student; there was no evidence of beaver activity. And this moss was found attached in its new location only 9 weeks after it was tagged. In both cases, the mosses were attached by rhizoids and were wrapped around fallen tree branches where they most likely were held in place by the flow of water. Several other fragments were found in new locations, but these lacked rhizoid attachments.



Figure 18. *Ursus americanus* catching salmon in Alaska stream. Dark patches of mosses can be seen by its feet, suggesting an opportunity for dispersal. Photo by J. Brew, through Creative Commons.

In experiments with *Fontinalis*, I have observed that stems with broken tips will often produce protonemata or several apical branches (Figure 19-Figure 20).

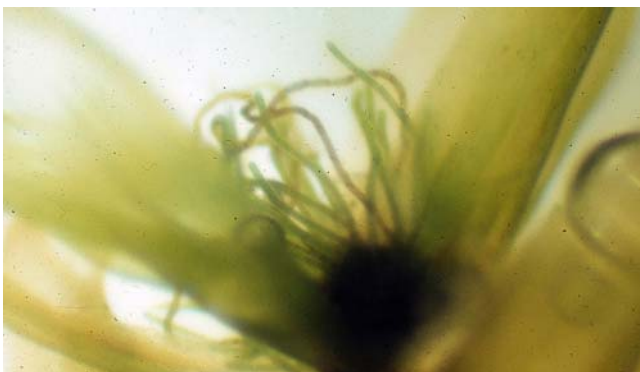


Figure 19. *Fontinalis hypnoides* broken shoot apex producing protonemata. Photo by Janice Glime.



Figure 20. *Fontinalis antipyretica* apical wound with new growth and rhizoids. Photo by Janice Glime.

In the winter, aquatic mosses can get frozen in the ice (Figure 21). When the ice breaks up, chunks may carry a number of fragments downstream where some may become impinged on suitable substrata.



Figure 21. Fragments of *Fontinalis dalecarlica* frozen in ice that has broken up in a New Hampshire, USA, headwater stream. Photo by Janice Glime.

Sayre (1945) demonstrated that connections of waterways could account for the dispersal of *Fontinalis* in a series of moraine ponds. Using Polymerase Chain Reaction (PCR) and involved amplification of DNA sequence with several ISSR primers, Korpelainen *et al.* (2004; 2013) found little variation in several bryophytes between lakes and concluded that *Fontinalis antipyretica* (Figure 20), *F. hypnoides* (Figure 19), and *Calliergon megalophyllum* (Figure 22) were dispersed by water between the lakes. This can occur by streams connecting lakes or by flooding that connects them. They did not rule out waterfowl, but found that the direction of flow and genetic patterns indicated that stream flow was a major contributor to the dispersal.



Figure 22. *Calliergon megalophyllum*, a species that is likely to be dispersed by water. Photo by Julita Kluša <daba.dziedava.lv>, with online permission.

Arts (1982) used circumstantial evidence to show that *Fissidens fontanus* (Figure 23-Figure 24) is dispersed by water. All the canals where he found them in Belgium and the Netherlands were fed by water from Maas and this source apparently dispersed them through the Albert Kanaal and the Zuid-Willemsvaart.



Figure 23. Canal with *Fissidens fontanus* growing on concrete (arrow). Photo by Michael Lüth, with permission.



Figure 24. *Fissidens fontanus* frond. Photo by Michael Lüth, with permission.

Fragments may be the most important means of dispersal in many aquatic bryophytes. For submersed species that produce submersed capsules, capsules are relatively rare and it is likely that most spores never lodge on a suitable substrate. As a result, some of these species are somewhat rare. *Dichelyma capillaceum* (Figure 25) is one such rare species in Europe (Hylander 1998). Only two populations are known with sporophytes. In Sweden it occurs along rivers, streams, and lakeshores – only in places that are inundated and then exposed annually. Hylander suggested that it was probably dispersed by fragments and more rarely through long-distance dispersal of spores.



Figure 25. *Dichelyma capillaceum* on a tree base in Europe where it gets flooded. Photo by Michael Lüth, with permission.

Antarctic researchers have used the RAPD technique to track populations and determine their genetic relatedness. For example, Dale *et al.* (1999) found *Hennediella heimii* (Figure 26) in Miers Valley, Antarctica, along melt streams within the valley, constituting a single large population, whereas it was distinct from populations in nearby valleys. The RAPD technique indicates that *Chorisodontium aciphyllum* (as *Sarconeurum glaciale*; Figure 9) from three locations on Ross Island, Antarctica, appear to all be from one population and differ genetically from populations elsewhere (Skotnicki *et al.* 1999a). Dispersal was apparently in small, meltwater drainage streams. *Bryum argenteum* (Figure 27), likewise, has apparently been transported in the Antarctic by water (Skotnicki *et al.* 1999b).



Figure 26. *Hennediella heimii* with capsules, a moss that gets transported by melt streams in the Antarctic. Photo by David T. Holyoak, with permission.



Figure 27. *Bryum argenteum*, a worldwide taxon that seems to be transported by water in the Antarctic. Photo by Dick Haaksma, with permission.

It appears that some species may respond adaptively to being submersed. *Leptobryum pyriforme* (Figure 28) produces rhizoidal gemmae (tubers; Figure 29) when the protonema grows in water (Schofield 1981), suggesting a possible secondary dispersal by water movement, or a way of surviving until the water recedes.



Figure 28. *Leptobryum pyriforme* with capsules. Michael Lüth, with permission.

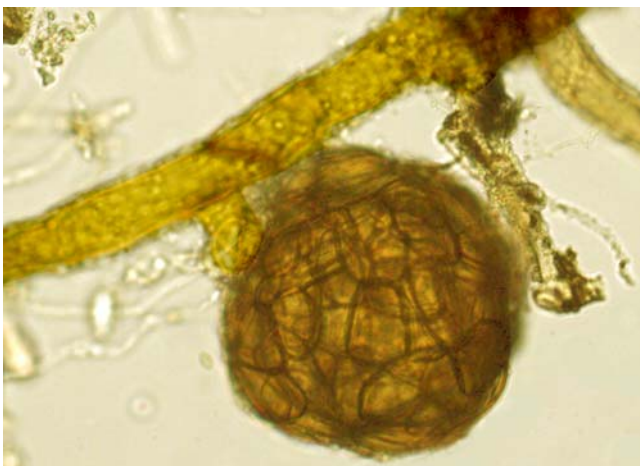


Figure 29. *Leptobryum pyriforme* rhizoidal tuber. Photo by Victoria Rozhina.

Water dispersal is a likely avenue for aquatic thallose liverworts. Patidar *et al.* (1986) studied effects of stream

velocity on the floating liverwort *Riccia fluitans* (Figure 30-Figure 31). They found that a decrease in number of sporophytes was related to increase in water velocity, a likely consequence of reduced fertilization. Nevertheless, increased vegetative dispersal is likely in this species.



Figure 30. *Riccia fluitans* stranded above water where it is also able to grow. Note the piece dangling from the colony at the bottom of the picture. This ramet can easily break away when the water level submerses this thallus again. Photo by Ralf Wagner at <<http://www.dr-ralf-wagner.de/>>, with permission.



Figure 31. *Riccia fluitans* showing dead portions that will decay and break the clone apart. Photo by Kristian Peters, with permission.

Splash Cups

Water dispersal is not confined to plants living in or near water. Some bryophytes take advantage of splashing raindrops for their dispersal, providing cups or platforms from which asexual propagules can be splashed. The best-known method of dispersal is that of the **gemma cup** or **splash cup**, commonly taught in introductory botany courses. Although the splash cup and splash platform are somewhat frequent as a means of dispersing sperm, they are relatively rare as mechanisms of propagule dispersal. Several bryophytes have specialized cups where the gemmae are produced and from which they are subsequently dispersed by raindrops (Figure 32, Figure 33). The splash cup mechanism seems to be engineered to maximize the distance its contents can splash, thus forming an effective dispersal mechanism with the help of raindrops. The significance of its size and shape was apparently not recognized until Buller (1942) described its function in the bird's nest fungus, *Cyathus*. Brodie (1951) followed up on

the observations of Buller and noted that splash cups commonly form 60-70° angles with the horizontal surface, the cups have a broad basal attachment, and the dispersed objects are lenticular. Gemmae of *Marchantia polymorpha* (Figure 32) can travel up to 120 cm when splashed from these cups, and Equihua (1987) suggests that this mechanism partly accounts for the worldwide distribution of this species. This ability to splash with water drops has made the species one of disdain for greenhouse owners who constantly find it invading their pots, spreading farther and farther from the original source through successive generations.



Figure 32. Lens-shaped gemmae of *Marchantia polymorpha*. Photo by Michael Lüth, with permission.

Gemmae in the splash cups of the moss *Tetraphis pellucida* (Figure 33) and the liverworts *Lunularia cruciata* (Figure 34-Figure 35) and *Marchantia polymorpha* (Figure 32) are lenticular. It seems to be a common feature for the splashing to carry the contents about 60 cm in *L. cruciata* and *M. polymorpha* (Brodie 1951), but in *T. pellucida*, they seem only to go about 10 cm (Kimmerer 1991). Brodie (1951) considered *T. pellucida* too frail to benefit from raindrops striking its apex, finding that the plants bent under the weight.



Figure 33. Gemma cups of the moss *Tetraphis pellucida*. Photo by Michael Lüth, with permission.



Figure 34. Gemmae in half-moon-shaped pouches of *Lunularia cruciata*. Photo by David T. Holyoak, with permission.



Figure 35. Pouch of *Lunularia cruciata* showing lenticular gemmae. Photo by Martin Hutten, with permission.

Stieha *et al.* (in prep.) quantified the production and dispersal of gemmae in the clonal thallose liverwort *Marchantia inflexa* (Figure 36). They found that these asexual propagules could move great distances during even a light rain, with some most likely leaving the parent clonal population. Further dispersal can occur in a stair-step fashion over time, providing long-distance dispersal. In this species, survival of female gemmae is greater than that of male gemmae.



Figure 36. *Marchantia inflexa*. Photo by Scott Zona, through Wikimedia Commons.

Animal Dispersal

The dispersal of vegetative parts by animals may be an important mode of travel, at least occasionally. Various insects use fragments of mosses and lichens to build "houses" that they carry on their backs.

Even mammals may eat (perhaps not intentionally) bryophytes, as indicated by ^{14}C studies on animal remains of late Pleistocene large herbivorous mammals (Ukrainitseva 1979). But we have no evidence that these bryophyte fragments remain viable after passing through the mammalian digestive tract.

Earthworms

Dispersal in the guts of earthworms (During *et al.* 1987; van Tooren & During 1988) can surely at times beat the 10 cm record for splashing in *Tetraphis pellucida* (Figure 33) reported by Kimmerer (1991); these and other invertebrates that eat bryophytes will deposit fragments in new locations. These could be distances of centimeters to hundreds of meters. Not only earthworms, but moles, voles, and ants have underground activities that can bring diaspores from their dormant state below ground to a position of activity above ground. Van Tooren and During (1988) found that eight species of bryophytes from the Netherlands appeared frequently in castings (Figure 37) from the earthworms *Allolobophora caliginosa*, *A. chlorotica* (Figure 38), and *Lumbricus terrestris* (Figure 39).



Figure 37. Earthworm castings on moss. Photo by Ken Gergle at Moss and Stone Gardens, with permission.



Figure 38. *Allolobophora chlorotica*, an earthworm that can transport bryophytes in its feces. Photo by Jacopo Werther, through Wikimedia Commons.



Figure 39. *Lumbricus terrestris* on mosses, a species known to ingest mosses and re-deposit them, still viable, in their feces. Photo by Michael Linnenbach, through GNU Free Documentation.

Since the light travels at most only a few centimeters into the soil, these diaspores remain dormant until some disturbance brings them to the surface and light. The species that survived the enzymes, crushing, and scarification of the earthworm guts, then grew to be identified, were *Bryum klinggraeffii* (Figure 40), *Dicranella schreberiana* (Figure 41), *Ephemerum recurvifolium* (Figure 42), *Pottia* spp., *Pottia lanceolata* (Figure 43), and *Weissia* spp. (Figure 44) (van Tooren & During 1988). *Bryum rubens* (Figure 45), common in the castings, never produces capsules in the area and presumably survived as rhizoidal tubers. Most of the other taxa probably also survived as vegetative diaspores except for *Pottia* sp. and *Weissia* sp., which probably originated from spores. Among these, tubers of *Bryum klinggraeffii* (Figure 40), *Bryum rubens* (Figure 45), and *Dicranella schreberiana* (Figure 41) successfully germinated, but in general, there was high mortality among tubers and other vegetative structures. Van Tooren and During suggested that spore survival was higher than vegetative diaspore survival in earthworm guts, but they did not have quantitative measures of this.



Figure 40. *Bryum klinggraeffii*, a species that survives earthworm guts. Photo by Des Callaghan, with permission.



Figure 41. *Dicranella schreberiana*, a species dispersed in earthworm castings in Europe. Photo by Michael Lüth, with permission.



Figure 42. *Ephemerum recurvifolium*, a species whose vegetative diaspores survive earthworm guts. Photo by Tomas Hallingbäck, with permission.



Figure 43. *Pottia lanceolata*, a species that survives earthworm gut, probably as vegetative diaspores. Photo by Michael Lüth, with permission.



Figure 44. *Weissia fallax*, member of a genus known from earthworm castings in Europe. Photo by Michael Lüth, with permission.



Figure 45. *Bryum rubens* showing rhizoidal tubers, a possible means of surviving earthworm guts. Photo by Jan-Peter Frahm, with permission.

Arthropods

Isopods

I suspect that isopods (pillbugs, sowbugs, wood lice, roly pollys) play a greater role in bryophyte dynamics than we understand. They make good experimental animals, and in our experiments, we have learned that both aquatic and terrestrial isopods readily eat some bryophytes (Figure 46-Figure 50), but avoid others, depositing their feces elsewhere. Some fragments can break off during the feeding and others are likely to be broken by their movements. We have not, however, observed any fragments being carried on their bodies and viability of mosses in their feces needs to be tested.



Figure 46. *Porcellio scaber* (isopod) eating *Pleurozium schreberi*. Photo by John Hribljan, with permission.



Figure 47. *Porcellio scaber* escaping from *Rhytidiadelphus triquetrus* that has been disturbed. Photo by John Hribljan, with permission.

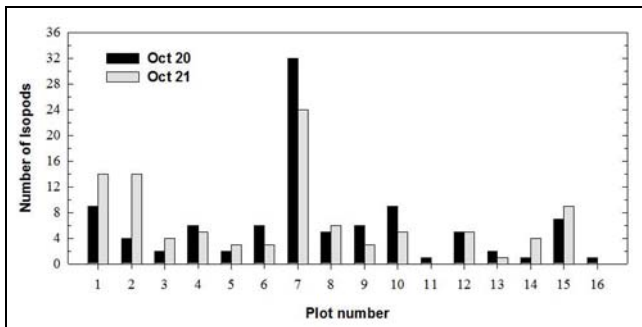


Figure 48. Comparison of abundance of *Porcellio scaber* in moss plots in the Keweenaw Peninsula of Michigan, USA, showing variability in numbers both spatially and daily. Graph by John Hribljan, with permission.



Figure 49. Evidence of eaten apical portions of *Pleurozium schreberi*, victim of *Porcellio scaber*. Photo by John Hribljan, with permission.



Figure 50. Evidence that *Porcellio scaber* prefers leaves to stems in feeding experiments on *Rhytidiadelphus triquetrus*. Photo by John Hribljan, with permission.

Mites (Acari)

Edwards (1978) found protonemal gemmae of *Schistostega pennata* (Figure 51) attached to the legs of mites. The gemmae, like the spores of this species, are very sticky (Ignatov & Ignatova 2001). While mites themselves most likely do not travel far, they can become passengers on other animals – birds and mammals – that might travel considerable distances. Risse (1986, 1987) suggested that this might also be a possible vector for rhizoid tubers, presumably because the mites move about amid the spaces in the soil.

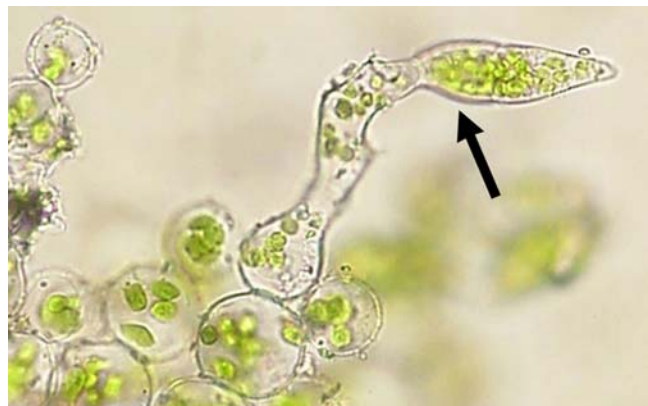


Figure 51. Protonemal gemma (arrow) of *Schistostega pennata*. Photo by Misha Ignatov, with permission.

Zhang *et al.* (2002) observed spider mites (*Halotydeus* sp.; Figure 52) eating the gemmae of *Octoblepharum albidum* (Figure 52) in Hong Kong. It is possible that some of these gemmae will get trapped among the hairs on the legs, thus getting transported by the mite. Others might be knocked off, falling to a new substrate.



Figure 52. *Halotydeus* sp. feeding on gemmae of *Octoblepharum albidum* in Hong Kong. Arrow indicates bases remaining where gemmae have been chewed. Photo by Li Zhang from Zhang *et al.* 2002, with permission.

Harvestmen

Some arthropods have an unusual mode of transporting bryophytes – they grow them on their bodies. These include liverworts on Neotropical harvestmen (Machado & Vital 2001).

Insects

Insects are often responsible for releasing small fragments of bryophytes (Lepp 2008). Larger insects can break dry bryophytes due to the insect weight, and a number of insects actually eat the bryophytes. Some live among the cushions where they often find food and thus move around, potentially transporting the fragments from a cushion to an open space.

Slocum and Lawrey (1976) report that the green lacewing larva (*Nodita pavidia*) carries about a "packet" of camouflage constructed of bits of lichen, lichen soredia, pieces of bark, pollen grains, fungal spores, moss gametophyte fragments, and other debris. They demonstrated that the lichen fragments were viable but did not test the mosses. It is likely that they not only were alive, but that some of these fragments also would land somewhere and grow. Larvae of Diptera (flies, especially crane flies) and Trichoptera (caddisflies) construct houses of various shapes and may incorporate bryophyte fragments in them, as will be discussed later in the chapter on aquatic insects.

Aquatic organisms can be dispersed by aquatic insects that carry adhering cells on their bodies (Stewart & Schlichting 1965, 1966; Stewart *et al.* 1970), but their role in bryophyte dispersal is mostly unknown. For example, some caddisfly larvae may construct their homes from mosses, leafy liverworts, or narrow thallose liverworts like *Riccia fluitans* (Figure 30; Glime 1978). When these homes (cases) are discarded, the bryophytes can potentially grow in this new location.

Cairns and Wells (2008) reported that the microcaddisfly *Scelotrichia willcairnsi* (Figure 53) in Australia fed on the moss *Platyhypnidium muelleri* (Figure 54), an activity that could permit transport of fragments that survive travel through the gut. But in addition, and more likely to survive, are fragments that they weave into their case. The case travels with the caddisfly, which may

travel considerable distance if it breaks loose from its substrate and becomes part of the drift.



Figure 53. The caddisfly *Scelotrichia willcairnsi* with *Platyhypnidium muelleri* case. Photo courtesy of Andi Cairns.



Figure 54. The moss *Platyhypnidium muelleri* with the caddisfly *Scelotrichia willcairnsi* showing numerous cases. Photo courtesy of Andi Cairns.

Weevil Gardens – A few insects disperse mosses in an unusual way. Certain weevils (Curculionidae) have pits on them where mosses are able to grow. This is the case for the moss *Daltonia angustifolia* (Figure 55) that attaches in pits on the hardened exoskeletons of weevils, including the weevil *Gymnopholus reticulatus* (Figure 55; Gradstein *et al.* 1984).

Gressitt and coworkers (1965, 1968) reported gardens on the backs of several species of weevils, including *Gymnopholus* spp. (Figure 55) among others. These weevils live in areas with moss cover on forest ridges and summits in eastern New Guinea (Gressitt *et al.* 1965, 1968). *Gymnopholus* species with epizoic bryophytes live more than three years and have hairs or specialized scales not present on species without plants growing on them (Gressitt & Sedlack 1970). In experiments where weevils were kept in cages, older weevils lost their plants, demonstrating the usefulness of these species as dispersal vectors. They are usually sedentary, but they can travel up to 0.25 km in half an hour by walking.



Figure 55. The moss *Daltonia angustifolia* living epizootically on the weevil *Gymnopholus reticulatus*. Photo courtesy of Rob Gradstein.

Ants – Rudolphi (2007) found that ants on stumps served as dispersal vectors, passively carrying the bryophyte dispersal units for a significant time. Rudolphi (2009) used experiments to demonstrate that the ant *Lasius platythorax* (Figure 56) may disperse the gemmae of *Aulacomnium androgynum* (Figure 57). Both the ants and the *A. androgynum* occur on dead wood in Sweden. When the ants were permitted to run over a moss tuft, gemmae adhered to 33% of the ants within only two minutes! Half the gemmae remained attached for about four hours. This is most likely passive dispersal, with no special adaptations by either organism. Since these are active organisms that can travel considerable distances quickly, this could be an important dispersal mechanism.



Figure 56. *Lasius platythorax*, an ant that disperses gemmae of *Aulacomnium androgynum*. Photo by April Nobile, through Creative Commons.



Figure 57. *Aulacomnium androgynum* gemmae, known to sometimes have dispersal by ants. Photo by Des Callaghan, with permission.

One interesting way that ants (*Formica rufa* group; Figure 58) contribute to dispersal is in their nest building. Heinken *et al.* (2007) sampled nesting material from 25 ant nest mounds in Germany. They found fragments of 20 bryophyte and 10 lichen species in these mounds. Among the bryophytes, wefts were particularly well represented, whereas tall turfs were poorly represented relative to their abundance. The researchers suggested that fragments lost along the way provided a means of dispersal. Other successful dispersal may occur among fragments in the mound when the mound decays. Healthy mounds with live ants do not provide a safe site for the bryophytes. The ants are active in maintaining the mound and keep burying the fragments. Any that do manage to remain at the surface are subject to greater drying than those on the surrounding soil. In addition to these problems, disturbance by the ants, birds, and even boars further dislodges them, interrupting growth and detaching the fragments.



Figure 58. *Formica rufa*, an ant that disperses bryophytes through its nest building. Photo by Richard Bartz, through Creative Commons.

The most common species on these ant mounds were *Hypnum cupressiforme* s.l. (Figure 143) in 16 of the 25 samples (Heinken *et al.* 2007). These accounted for 67.5% of the fragments. In addition, *Brachythecium* spp. (Figure 142) and *Pleurozium schreberi* (Figure 59) were often abundant. Species differed by forest type. Five of the 20 bryophyte species rarely produce any spores or vegetative structures, making fragments important in their dispersal. The territory size for this species ranges 200-1500 m² and the travelling ranges extend 20-30 (65) m from the nest, making a reasonable dispersal distance.



Figure 59. *Pleurozium schreberi*, a moss known from ant mounds. Photo by Janice Glime.

Modern genetic techniques permit us to learn even more about insect roles. Korpelainen *et al.* (2011) studied *Barbilophozia attenuata* (Figure 60) in an area traversed by ant trails, using spatial genetic structure to unravel the history of the liverwort dispersal. They found significant kinship of colonies along the trails up to 8 m. At distances greater than 25 m, kinship correlation was nearly zero. Gemmae were most important up to 8 m, but spores were important for distances of 25 m or greater. Plants on logs and other raised surfaces can achieve even greater distances by spores. They considered that the large gemmae permitted greater opportunity for establishment than the small sexual spores and gemmae account for the aggregated distribution of the species in the study area. They also concluded that gemmae are favored over spores in areas with frequent disturbance, such as ant trails. Nevertheless, at greater distances, spores become important.



Figure 60. *Barbilophozia attenuata* with apical gemmae. Photo by Michael Lüth, with permission.

Lepidoptera – Larvae of *Aenetus virescens* (Figure 61) feed on the leaves and rhizoids of both live and dead mosses and liverworts, among other things (Grehan 1984). These bryophytes have the potential of being dispersed in feces, but tests must be made to see if they survive the gut. It is also possible that fragments adhere to these larvae, thus being dispersed.



Figure 61. *Aenetus virescens* adult, looking perfectly suited to living among bryophytes, where it might complete its emergence, but it lives only 48 hours as an adult. Its larvae feed on bryophytes, among other things. Photo by Tony Wills, through Wikimedia Commons.

Molluscs

Mollusks such as slugs eat bryophytes, but their sticky surfaces also cause fragments to adhere, effecting their dispersal. The moss *Orthodicranum flagellare* (Figure 2) lives on logs and stumps where snails can readily gain access and contribute to dispersal of the flagelliform branches that serve as propagules (Stolzenburg 1995). Kimmerer and Young (1995) found that this species depends on its asexual brood branches to colonize new logs, with slugs as their primary dispersal vector. In fact, the propagules adhere to the slime trails, with evidence that the slugs (*Philomycus* sp.; Figure 62) can transport them at least 23 cm. However, the distance is more commonly only about 3.7 cm. The slime helped the propagules adhere to the substrate without interfering with success of germination.



Figure 62. *Philomycus carolinianus* on a log, crawling over worms. Photo by Rebekah D. Wallace, through Creative Commons.

Aquatic molluscs also facilitate the dispersal of bryophytes. Both *Fissidens fontanus* (Figure 24) and *Leptodictyum riparium* (Figure 63) are known from the shells of mussels, a moving substrate that is likely to drop off fragments as it moves (Neumann & Vidrine 1978). Species of *Fissidens* are especially vulnerable to grazing by snails and slugs (Figure 64), so it is likely that fragments also get dispersed in the feces of the bodies of these molluscs.



Figure 63. *Leptodictyum riparium*, a moss that is known to grow on mussel shells. Photo by Michael Lüth, with permission.



Figure 64. *Fissidens* sp. being traversed by a slug. Photo by Janice Glime.

Amphibians

Like slugs, most amphibians have moist, sticky skin (Evans & Brodie 1994). Therefore, it is likely that bryophyte fragments and propagules get broken off as they traverse the bryophytes and that many of these same fragments and propagules get transported to new locations. My own pet frog was usually covered by empty seed coats dropped by the finches that shared the room. Evans and Brodie found moss fragments were among the debris they washed from amphibians at the beginning of their sampling. In their experiments, Evans and Brodie found that *Dyscophus antongilii* and *D. guineti* had the strongest glue among the eleven amphibians tested. D. Bruce Means has captured this adherence to *Ceuthomantis smaragdinus* in the image below (Figure 65).

Figure 66 through Figure 71 demonstrate some of the variety of anurans that are able to carry bryophyte fragments. These six images were selected from my collection of 494 anuran images based on discernible adhering debris, giving a very crude estimate of the frequency of such passage. Figure 72-Figure 73 demonstrate that salamanders are also able to carry bryophytes that adhere to the sticky surface.



Figure 65. *Ceuthomantis smaragdinus* with several fragments of bryophytes adhering. Photo by D. Bruce Means, through public domain, USFWS.



Figure 66. *Trachycephalus resinifictrix* with debris attached to its breast. Photo by John White, with permission.



Figure 67. *Craugastor bransfordii* with an adhering bryophyte at the arrow. Photo by Jason Folt.



Figure 68. *Oophaga pumilio* on moss, with debris adhering to its skin. Photo by Brian Gratwicke, through Creative Commons.



Figure 69. *Rana arvalis* with a bryophyte fragment adhering to its leg. Photo by Petr Balej, with permission.



Figure 70. *Ascaphus truei* with an adhering moss fragment on its back. Photo by James Bettaso, USFWS, through public domain.



Figure 71. *Bufo bufo* with adhering plant material, demonstrating that even the dry skin of a toad can carry plant fragments. Photo by Karamel, through Wikimedia Commons



Figure 72. *Hynobius tokyoensis* carrying a bryophyte fragment on its head. Photo ©Henk Wallays, through Creative Commons.



Figure 73. *Nototriton abscondens* with large bryophyte fragments on its back. Photo by Eduardo Boza Oviedo, with permission.

Turtles

I have experienced this dispersal first-hand by inference. When I (Glime, unpubl) grew *Conocephalum conicum* (Figure 74) and *Fissidens* (Figure 75) in my garden room in the company of a box turtle (*Terrapene*; Figure 76), both bryophytes spread quickly around the room, something they never did in the absence of the turtle. But eventually the zebra finches discovered the liverwort and each day it grew smaller, with triangles cut from its edges. Alas, the birds seemed to be agents of destruction and not dispersal because *C. conicum* soon disappeared completely. The *Fissidens* likewise stopped spreading and within some months it too disappeared.

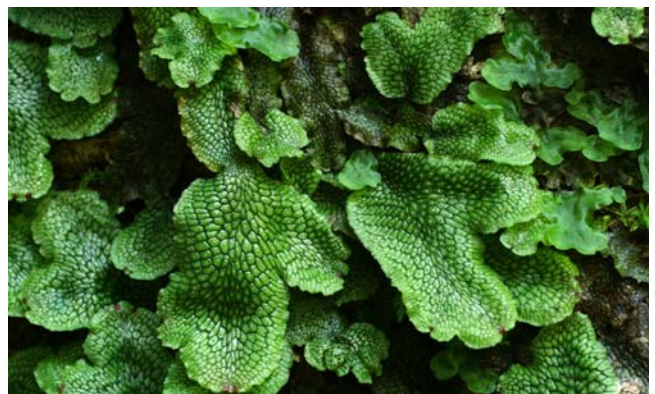


Figure 74. *Conocephalum conicum*, a liverwort that is eaten by birds and carried by turtles. Photo by Robert Klips, with permission.



Figure 75. *Fissidens taxifolius*, a moss that seems to be carried by turtles. Photo by David Holyoak, with permission.



Figure 76. *Terrapene carolina*, a potential bryophyte dispersal vector. Photo through Wikimedia Commons.

McGregor (1961) has a more documented story. He found living thalli of *Riccia rhenana* (Figure 77) on the carapace of a snapping turtle (*Chelydra serpentina*; Figure 78) that had ventured nearly 1 km from the nearest pond. This liverwort species grows among cattails, sedges, rushes and grasses of shallow water where it multiplies by growth and division of thalli, mostly in April. The thallus dries up to its growing apex in summer, and McGregor observed it in that dry state for up to 33 days, when it was rehydrated by rains and resumed growth. Its ponds often freeze solid, freezing the thalli in ice. Once again, the thalli die except the growing apex. McGregor reports that these thalli can survive more than five weeks in the ice.



Figure 77. *Riccia rhenana*, a liverwort known to be carried by a snapping turtle. Photo by Jan-Peter Frahm, with permission.



Figure 78. *Chelydra serpentina* (snapping turtle) female searching for a nesting site. Photo by D. Gordon E. Robertson, through Wikimedia Commons.

Birds

Aquatic organisms living in isolated wetlands could have real difficulty being dispersed. But Figuerola and Green (2002) found that widespread distributions of aquatic organisms typically coincide with pathways of migratory waterbirds. They considered that small propagule size would favor dispersal, but we have seen that birds are important dispersers of bryophyte fragments (Lewis *et al.* 2014). Behling *et al.* (2002) have further demonstrated dispersal through **endozoochory** – ingestion of fragments by birds. Birds travel long distances, and rather quickly. Their frequent stops for food makes them ideal dispersal agents because in most cases any adhering bryophyte parts won't be in the atmosphere for very long. (See further details of long migration flights in Chapter 4-8.)

The introduction of the aquatic liverwort *Ricciocarpos natans* (Figure 79) into Norway may be the result of transport by waterfowl or some other form of epizooic transport (Skulberg 1978). This has been shown for a number of algae that travel on the feathers and feet of ducks, arriving in viable condition (Schlichting 1958). Both mechanisms seem reasonable for bryophyte spores and leaf fragments, or even small branches.

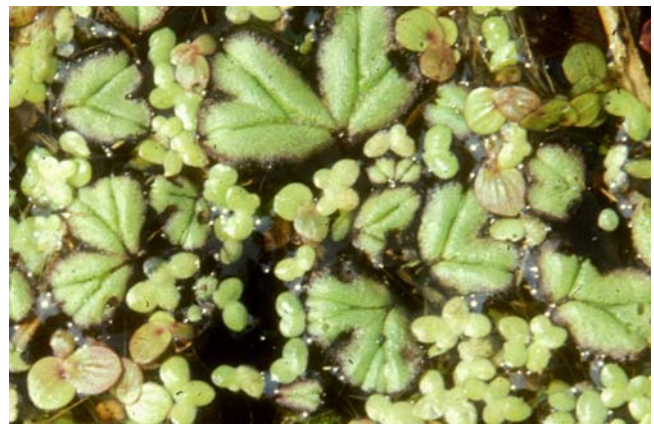


Figure 79. Thalli of *Ricciocarpos natans* floating with the duckweeds *Lemna minor*, *Wolffia* sp., and *Spirodela polyrrhiza*. Since duckweeds are common foods for waterfowl, it is likely that *Ricciocarpos* gets mixed in with the food and stuck to feathers or feet as the birds wade and eat. Its may also be eaten, if only inadvertently, and could possibly be dispersed in feces. Photo by Janice Glime.

The **Kelp Gull** (*Larus dominicanus*; Figure 80) in the Argentine Island region of the Antarctic uses bryophytes and other plant material for building its nest (Parnikoza *et al.* 2012). Some of these bryophytes are able to establish in their new locations. If the gull can survive a long flight, most likely the bryophyte can as well.



Figure 80. *Larus dominicanus* (Kelp Gull), a bird that spreads bryophytes by putting them in its nest in the Antarctic. Photo by Steve and Jem Copley, through Creative Commons.

McGregor (1961) actually found evidence that ducks indeed disperse living bryophytes. A fragment of *Riccia fluitans* (Figure 30) was attached to a feather at the back of the neck of a pintail duck (*Anas acuta*; Figure 81) that was soon to become a hunter's dinner. The duck was intercepted just before it descended to land on the Kansas River.

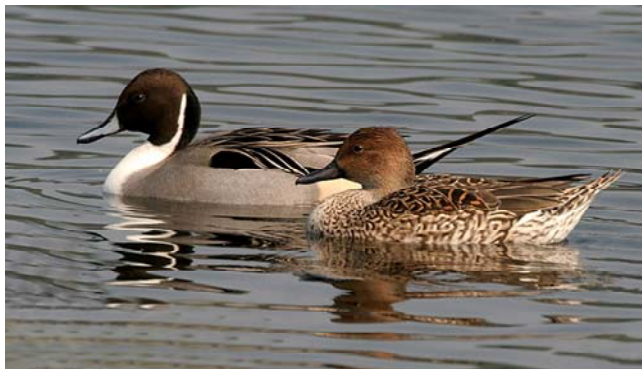


Figure 81. Male and female Northern Pintails (*Anas acuta*). Photo by J. M. Garg, through Wikimedia Commons.

In Hungary, geese (Figure 82) are known to carry such fugitives as *Riccia frostii* (Figure 83) on their feathers, feet, or muddy bills, making these liverworts common – you guessed it – along goose trails (Crum 1973). But might they also be transported in the feces? Bryophytes such as *Riccia fluitans* (Figure 30-Figure 31) exist among duckweeds (Lemnaceae) and thus will almost certainly be eaten along with them. With 0.7 kg of defecation (French & Parkhurst 2009) occurring every 20 minutes (Bowen & Valiela 2004), there is considerable opportunity for transport, albeit not very far if it has only 20 minutes of residence time. Jasmin *et al.* (2009) found that bryophytes increased in areas of goose foraging in the Arctic, but this may have been due to an increase in available habitat.



Figure 82. Domestic goose (*Anser*). These are among the known vectors of bryophytes through fragments stuck to feathers or feet. Note bits of mud on lower feathers and feet. Photo through Wikimedia Commons.



Figure 83. *Riccia frostii*, a liverwort that is a known goose hitchhiker. Photo by Rosemary Taylor, with permission.

Crows seem to be favorites as the villains in moss destruction. Misha Ignatov (Bryonet 23 February 2013) reports seeing the rare (in Moscow) moss *Dicranum viride* (Figure 84) scattered over the ground rather than in place on the tree trunks. As he wondered who the destructive villain was, he heard crows overhead, then noticed a number of crow nests. He concluded that the crows were the likely vandals. He hoped that they might be forgiven if in the process the crows succeeded in dispersing the mosses to new locations where they could establish.



Figure 84. *Dicranum viride* on tree trunk in Michigan, USA. Photo by Janice Glime.

Erkamo (1976) reported observations of mosses being upturned, especially on flat, open rocks. These were mostly only a few cm in size, but some were 10-15 cm across. He considered the agents of this upheaval to be possible by voles, pheasants, seagulls, or crows, but considers crows (Figure 85) to be the most likely. He has actually seen crows in such activity, and considered that they were probably looking for food such as insects or worms under the moss cover. Erkamo lamented the destruction of beautiful rock scenery that will most likely take years to recover.



Figure 85. *Corvus brachyrhynchos*, a crow that scatters mosses to find food. Photo by Walter Siegmund, through GNU Free Documentation.

Blackbirds (*Turdus merula*; Figure 86) have found another use for bryophytes that is likely to disperse them. Robin Stevenson (Bryonet 15 April 2010) reported observing **displacement activity** in this species. He observed a male throwing clumps of moss off a rooftop, alternating the activity with altercations with another blackbird. This displacement behavior was most likely part of a fight over territory and the mosses permitted them to take a break that prevented them from killing each other. The battered mosses included *Grimmia pulvinata* (Figure 87), *Hypnum cupressiforme* (Figure 88), and *Syntrichia montana* (Figure 89).



Figure 86. The Blackbird, *Turdus merula*, resting among lichens. Photo by Mario Modesto Mata, through GNU Free Documentation.



Figure 87. *Grimmia pulvinata* (Grey-cushioned Grimmia), a rooftop species that was thrown off by quarrelling blackbirds. Photo by Barry Stewart, with permission.



Figure 88. *Hypnum cupressiforme* var. *cupressiforme*, a species tossed from a rooftop by quarrelling blackbirds. Photo by David Holyoak, with permission.



Figure 89. *Syntrichia montana*, a species tossed about by quarrelling blackbirds. Photo by Barry Stewart, with permission.

Terrestrial bryophytes may get transported, at least for short distances, by bird behavior. For example, blackbirds (*Turdus merula*; Figure 86) forage among mosses to find insects or worms, tossing them aside to gain access (Davison 1976). It is likely that such food items and earthworms are closer to the surface under mosses where the moisture is greater. Davison reports that *Mnium hornum* (Figure 90) and *Polytrichastrum formosum* (Figure 91) may be tossed 1-2 m in these activities. In an area of 5 sq m, Davison found that 34 clumps with an average diameter of 2 sq cm were displaced in this way over a two-month period in Great Britain. Furthermore, an additional 18 clumps were moved into that same 5 sq m during the same time period (October-November).



Figure 90. *Mnium hornum*, a moss that can be a victim of crow scavenging. Photo by Janice Glime.



Figure 91. *Polytrichastrum formosum*, a moss often disturbed by crows seeking food. Photo by Michael Lüth, with permission.

Gathering bryophytes for nests is a likely means of dispersal for nearly every kind of nest in which bryophytes are used, e.g., the Picaflor Rubi (*Sephanoides sephaniodes*; Figure 92-Figure 93) and White-sided Hillstar (*Oreotrochilus leucopleurus*) construct their nests primarily of mosses, especially those with falcate leaves (Calvelo *et al.* 2006). Fragments are likely to be dropped on the way, and many more are broken off or dropped or discarded during the construction of the nest and subsequent usage. For some, the lofty position of a nest in a tree provides the advantage of more opportunity to gain access to air movements that can carry the fragments even further.



Figure 92. Picaflor Rubi (*Sephanoides sephaniodes*), a bird related to the hummingbird that uses bryophytes to build its nest. Photo by Suemili, through Wikimedia Commons.



Figure 93. Picaflor Rubi (*Sephanoides sephaniodes*) on nest that is constructed of mosses, showing how its coloration blends with the moss. Photo by Diucón, through GNU Free Documentation.

When Surtsey was colonized after its ascension from the sea, the moss *Racomitrium* (Figure 94) was among the first invaders (Magnússon *et al.* 2009). The Lesser Black-backed Gull (*Larus fuscus*; Figure 95) invaded the island, forming a dense colony. Its primary nesting material was *Racomitrium*, but it is unclear if it was brought to the island by the birds or it arrived by fragments or spores and spread.



Figure 94. *Racomitrium lanuginosum*, one of the first mosses to arrive on Surtsey when it arose as a volcanic island. Photo by Juan Larrain, with permission.



Figure 95. *Larus fuscus* (Lesser Black-backed Gull) adult and juvenile, probably dispersal agents for *Racomitrium* sp. to Surtsey. Photo by Pline, through Wikimedia Commons.

Even when bryophytes are not transported to make nests, the nearness of a nest to bryophytes increases the chances that the bryophytes will become dislodged, and some may adhere to the birds. For example, the Peg-billed Finch (*Acanthidops bairdi*) is a rare bird in Costa Rica and Panama (Elizondo C. 2000). It has rarely been observed, but Mathias Jaschhof was able to photograph four fledglings in the nest (Figure 96). The nest was built in myrtle (*Vaccinium consanguineum*) and consisted of a bulky cup developed from *Frullania* sp. (Figure 97) with amendments of *Leptodontium* sp. (Figure 98), *Pilotrichella*, and *Plagiochila* sp. (Figure 100) as well as fruticose lichens and a mix of unidentified leafy liverworts and mosses (Elizondo C. 2000). The egg chamber had a layer of fern rhizomes, a thin layer of grass inflorescences, and finally an external layer of *Thuidium* sp. (Figure 105).

This latter layer may extend to the outside of the nest and may be surrounded by *Frullania*.



Figure 96. *Acanthidops bairdi* (Peg-billed Finch), a rare bird that builds a cup-shaped nest, sometimes in moss banks, as seen here. Photo by Mathias Jaschhof, with permission.



Figure 97. *Frullania*, leafy liverwort that is predominant in the nest of the Peg-billed Finch (*Acanthidops bairdi*). Photo by Li Zhang, with permission.



Figure 98. *Leptodontium*, a secondary moss in the nest of the Peg-billed Finch (*Acanthidops bairdi*). Photo by Felipe Osorio Zúñiga, with permission.



Figure 99. *Pilotrichella* sp., a minor component of nests of the Peg-billed Finch (*Acanthidops bairdi*). Photo by Lena Struwe, through Creative Commons.



Figure 100. *Plagiochila adianthoides*, member of a genus used as a secondary bryophyte in nests of the Peg-billed Finch (*Acanthidops bairdi*). Photo by Michael Lüth, with permission.

Mammals

The role of mammals in dispersal of propagules seems to have gotten less attention than it deserves. Only recently are we seeing documentation that mammals can serve as dispersal vectors through feces, fur, and hooves, and in some habitats these may play a major role. Among these dispersal units are fragments that cling easily to the fur and feathers of some animals. Dispersal of fragments is most likely more important than we have considered (Heinken *et al.* 2001).

Rodents

I have blamed the chipmunks in my moss garden for tearing up my recent moss plantings. They seem to like frolicking across the bryophytes, and more than occasionally the bryophytes end up upside down as the chipmunks (Figure 101-Figure 102) kick them up or drag them with their feet. They seem to especially like *Leucobryum glaucum* (Figure 103-Figure 104) and *Thuidium delicatulum* (Figure 105). At least those are the most likely to get torn up in my garden, and one chipmunk insisted on making an entrance to a burrow in the middle of the *T. delicatulum*, destroying the integrity of the mat, hence causing its death. *Leucobryum* species have the ability to develop rhizoids on the upturned surface that contacts the soil (Figure 104) and may recover as a moss ball. Mine did not. Gray squirrels (Figure 106), and certainly others, have the same potential to serve as dispersal agents.



Figure 101. *Tamias sciurus* (eastern chipmunk) is responsible for kicking up loose mosses and most likely transports fragments. Photo by Oleksii Voronin, through Wikimedia Commons.



Figure 102. *Tamias sciurus* (eastern chipmunk) with bark stuck to its fur, showing how easily it could transport bryophyte propagules and fragments. Photo by Janice Glime.



Figure 103. Moss garden showing upturned *Leucobryum glaucum* at lower left and mist netting covering clumps to prevent further upheaval. Photo by Janice Glime.



Figure 104. *Leucobryum glaucum* with leaf rhizoids (arrow) that develop after the clump has been overturned. Photo by Kristian Peters, through Wikimedia Commons.



Figure 105. *Thuidium delicatulum*, a moss that a chipmunk used to make an entrance to reach its underground tunnels. Photo by Bob Klips, with permission.



Figure 106. Eastern gray squirrel (*Sciurus carolinensis*) amid mosses. This frisky animal is a likely dispersal agent for gemmae and fragments, especially when scratching to grab seeds, as seen here. Photo by Janice Glime.

In the Arctic, rodents, including moles and lemmings, eat the bryophytes (Ericson 1977), so dispersal of spores and fragments in their whiskers and fur is likely. Hribljan (unpubl) has cultured feces of rodents, collected from Alaska, that had protonemata germinate from them (Figure 107). It is likely that these came from fragments that were present in the feces, but could also have been from spores. Kimmerer and Young (1996) suggested that rodent activity may help *Orthodicranum flagellare* (Figure 2) disperse in two ways, by helping to produce gaps among the bryophytes on the logs and possibly by carrying the flagelliform propagules among the locations visited. In this regard, squirrels and chipmunks are likely agents. Could it be that they also inadvertently eat bryophytes as they forage and thus carry them in their guts? At the very least, they probably dislodge epiphytes, aiding their dispersal.



Figure 107. Protonemata and young gametophores germinated from microtine rodent scat collected in Alaska. Photo by John Hribljan, with permission.

Ericson (1977) showed that many of the most abundant forest mosses in northern Sweden are a preferred food for *Myopus schisticolor* (wood lemming; Figure 108). *Ptilidium ciliare* (Figure 109) and *Plagiothecium denticulatum* (Figure 110) are rejected, as are most herbaceous species. When the snow is gone, they feed on green tips of mosses, whereas when they are living under snow the lemmings bite the shoots off at the base. In 1974 and especially in 1975, following heavy grazing in 1973, *Dicranum scoparium* (Figure 111) spread to areas where no *D. scoparium* occurred in 1973. These rodents appear to have been the agents of both fragmentation and dispersal.



Figure 108. *Myopus schisticolor* (wood lemming) by its path amid *Hylocomium splendens*. Photo by Risto S. Pynnönen, through Wikimedia Commons

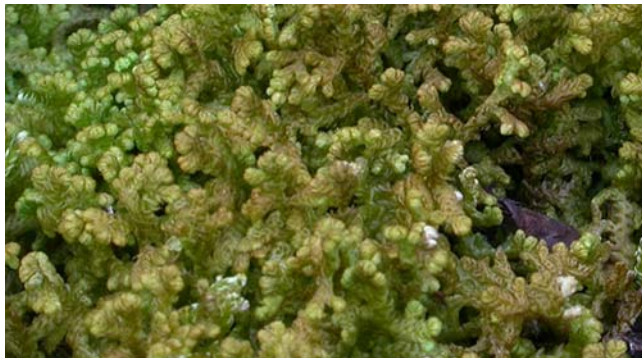


Figure 109. *Ptilidium ciliare*, a leafy liverwort rejected by the wood lemming (*Myopus schisticolor*). Photo by Li Zhang, with permission.



Figure 110. *Plagiothecium denticulatum*, a moss rejected by the wood lemming (*Myopus schisticolor*). Photo by Michael Lüth, with permission.



Figure 111. *Dicranum scoparium*, a moss most likely distributed by rodents in northern Sweden. Photo by Janice Glime.

Eskelinen (2002, 2004) likewise demonstrated that mosses are preferred food of the wood lemming in northern Finland, and that they also are selective. They consume *Dicranum* spp. (Figure 111) and *Polytrichum* (Figure 112- Figure 113) in greater quantities than would be expected, but avoid *Hylocomium splendens* (Figure 108) and *Pleurozium schreberi* (Figure 59). Nevertheless, Ericson (1977) found that *H. splendens* diminished, presumably due to rodent consumption. Eskelinen (2002, 2004) suggested the preference for *Polytrichum* and *Dicranum* may relate to their higher N content. If so, preferences may change with habitat and available food choices.



Figure 112. *Polytrichum commune* var *commune*, demonstrating the clone that can result from its branching rhizomes. Photo by David Holyoak, with permission.



Figure 113. *Polytrichum juniperinum*, a moss that spreads by rhizomes. Photo by Janice Glime.

Ericson (1977) followed the changes in moss cover in Scandinavia for four years and discovered that rodents played a major role in the changes. Only the mosses on windthrows and tree stumps maintained constant cover. The fascinating realization was that different species of bryophytes seemed to suffer declines and increases in different years. In 1974, *Ptilium crista-castrensis* (Figure 114) suffered 73% reduction and *Dicranum scoparium* (Figure 111) suffered 57%. However, in 1975, the strongest decrease was in *Hylocomium splendens* (Figure 108), which suffered 49% reduction, while *P. crista-castrensis* increased 43% and *D. scoparium* increased 70%! Ericson felt that this might indicate increased growth as a response to fragmentation caused by grazing. However, to increase cover values so significantly, it would seem that at least some dispersal must have been effected.



Figure 114. *Ptilium crista-castrensis*, a preferred moss for rodent consumption. Photo by Janice Glime.

Ericson (1977) felt that several types of regeneration were common for these species. *Polytrichum commune* (Figure 112) and *P. juniperinum* (Figure 113), as well as others, can recolonize from protonemata, juvenile plants, and rhizoid fragments (Meusel 1935, Wigglesworth 1947). *Hylocomium splendens* (Figure 108; Correns 1899) and species of *Dicranum* (Figure 111; Meusel 1935) grow easily from broken parts of stems, and *Polytrichum commune* and species of *Dicranum* regenerate from isolated leaves (Correns 1899). Callaghan *et al.* (1978) pointed to the need for *Polytrichum commune* to reproduce by underground branching into clones because of its finite life expectancy. *Hylocomium splendens* solves the problem of life expectancy by producing new shoots in a stair-step fashion, with the oldest part of the plant senescing and decomposing (Callaghan *et al.* 1978), a feature seen also in *Pseudocalliergon trifarium* (Figure 115; Bisang *et al.* 2008). However, if the young branch shoot of *Hylocomium splendens* is damaged, the entire plant will die (Callaghan *et al.* 1978). On the other hand, it seems to have a low branching rate for the main stem, limiting its clonal growth.

Bank voles (*Clethrionomys glareolus*) include small quantities of mosses in their diets (Watts 1968). Bank voles were caught in the act of eating mosses in The Netherlands. Andrew Spink was able to capture these on film (Figure 116).

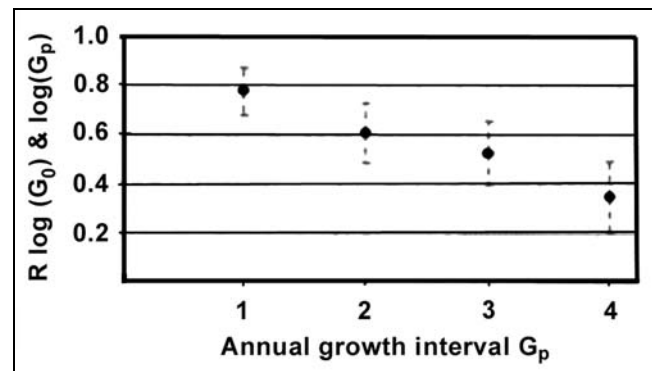


Figure 115. Diminishing growth rates of *Pseudocalliergon trifarium* through four years of growth. Redrawn from Bisang *et al.* 2008.



Figure 116. Bank vole eating mosses and most likely carrying fragments from one place to another. Photo by Andrew Spink, with permission.

Flying Fox

The spectacled flying fox (*Pteropus conspicillatus*; Figure 117), a fruit bat, passes bryophyte fragments in its feces (Figure 118-Figure 119), including chloronemata, rhizoids, and shoots (Parsons *et al.* 2007). These are capable of germinating (Figure 120) and may even benefit from nutrients in the adhering feces. Fifteen families of bryophytes were represented in these feces. Among the 48 fragments cultured, 52% germinated, producing rhizoids or shoot extensions. Even rotifers among the bryophytes were still alive. Included among the species were *Metzgeria* sp. (Figure 121), *Acroporium* sp. (Figure 122), *Leucobryum juniperoideum* (Figure 123, and *Racopilum* sp. (Figure 124). The germination rate was higher from samples taken during the early part of the season (17 out of 28 fragments) compared to those taken in the later part of the season (7 out of 20). This could represent a shift in diet, change in brittleness of bryophytes (resulting from desiccation) that changes ease of fragmentation, or a change in viability of the bryophytes. It is likely that the bryophytes were eaten unintentionally along with fruit.

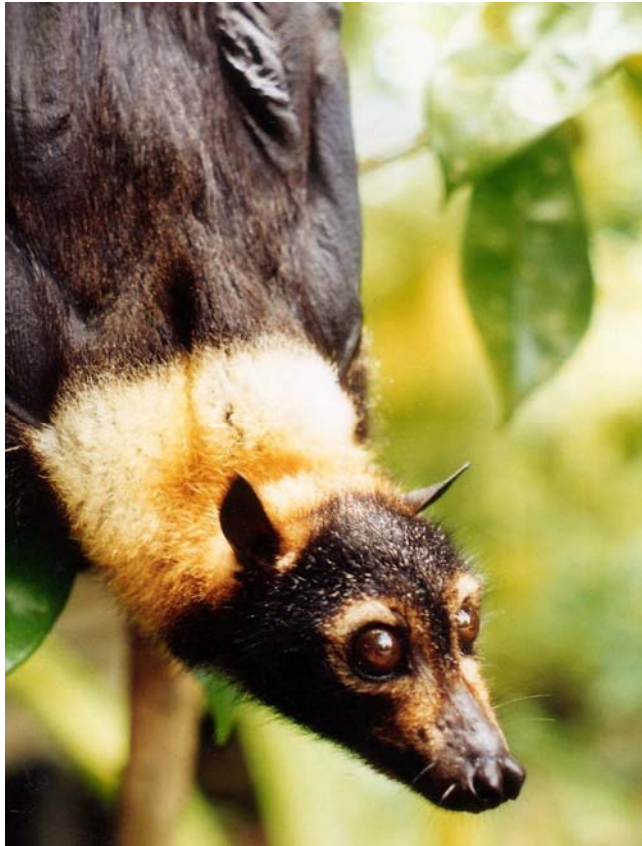


Figure 117. Spectacled flying fox (*Pteropus conspicillatus*). Photo courtesy of Andi Cairns.



Figure 118. Splat (feces) of flying fox on leaf. Photo courtesy of Andi Cairns.



Figure 119. Jennifer Parsons with flying fox splat trap. Photo courtesy of Andi Cairns.



Figure 120. Culture tube with flying fox feces. Photo courtesy of Andi Cairns.

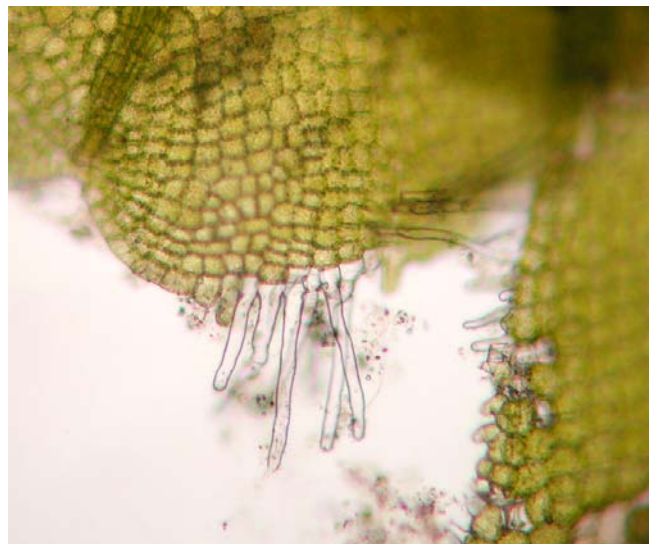


Figure 121. *Metzgeria* germinating from flying fox feces. Photo courtesy of Andi Cairns.

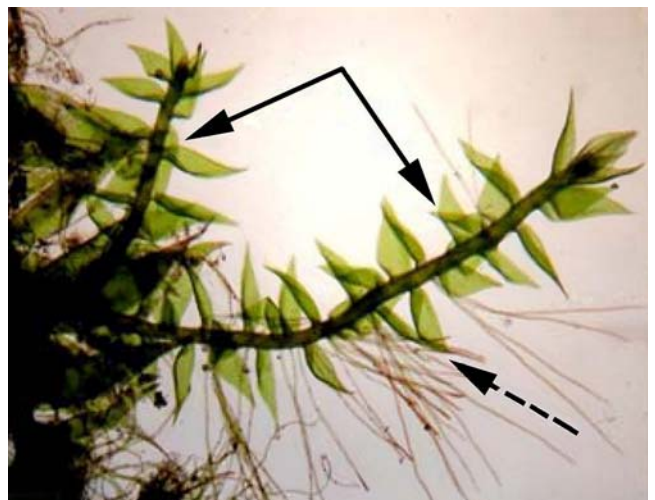


Figure 122. *Acroporium* sp. feces from flying fox. Solid arrows indicate new shoots; dashed arrows indicate rhizoids. Photo by Andi Cairns.



Figure 123. *Leucobryum juniperoideum* leaf fragment germinating from flying fox feces. Photo courtesy of Andi Cairns.



Figure 124. *Racopilum* sp. germinated from flying fox feces (splat). Photo courtesy of Andi Cairns.

Lessons from a Dog

Heinken (2000) conducted an interesting and most instructive study on dispersal of fragments by using a dog. Dogs act as good surrogates to demonstrate the ability of diaspores to adhere to fur, but their habit of wallowing on the ground is unusual among many wild mammals, making some predictions limited. In one year, Heinken walked his dog 49 times in the forest near his home in Germany. He found no seasonal differences in fragment attachments of bryophytes compared to the seasonal pattern observed for seed plant diaspores.

The forest used in the dog study had 20 species of bryophytes occupying 1% of the cover (Heinken 2000). The dog presented 29 bryophyte stem fragments from at least 10 bryophyte species. All the stem fragments had leaves and most had terminal buds. Only 13 of the fragments had branches and these were often numerous. The most frequent species were *Eurhynchium hians* (Figure 125) and *Ceratodon purpureus* (Figure 126). Other taxa included *Barbula* sp, *Amblystegium varium* (Figure 127), *Hypnum cupressiforme* (Figure 143),

Eurhynchium praelongum (Figure 128), *Plagiomnium* sp, *Rhynchostegium* cf *megapolitanum* (Figure 129), *R. murale* (Figure 130), and *Rhytidiadelphus squarrosus* (Figure 131). On the other hand, two species [*Atrichum undulatum* (Figure 132), *Mnium hornum* (Figure 90)] that were frequent in the study area were not represented at any time on the dog's fur.



Figure 125. *Eurhynchium hians*, one of the two most common species on dog fur in a German experiment. Photo by Michael Lüth, with permission.



Figure 126. *Ceratodon purpureus*, one of the two most common species on dog fur in a German experiment. Photo by Michael Lüth, with permission.



Figure 127. *Amblystegium varium*, a species found on dog fur in a German experiment. Photo by Jan-Peter Frahm, with permission.



Figure 128. *Eurhynchium praelongum*, a species found on dog fur in a German experiment. Photo by Michael Lüth, with permission.



Figure 129. *Rhynchoszegium megapolitanum*, a species found on dog fur. Photo by Michael Lüth, with permission



Figure 130. *Rhynchoszegium murale*, a species found on dog fur in a German experiment. Photo by David Holyoak, with permission.



Figure 131. *Rhytidadelphus squarrosus*, a species found on dog fur in a German experiment. Photo by Brian Eversham, with permission.



Figure 132. *Atrichum undulatum*, a moss that did not adhere to dog fur in a German experiment. Photo by Janice Glime.

Sources of the adhering bryophytes were primarily tree trunks, walls, paved places in the city, a grassland plot, and the lawn of the owner (Heinken 2000). The dog would frequently wallow on the ground, then shake and groom himself to remove annoying diaspores, especially seeds. The bryophytes that adhered were primarily wefts or short turfs with acute and often erect or squarrose leaves. Tall turf species with rounded leaves were very under-represented. Mats were likewise rare. Loose wefts, on the other hand, seemed to hitch a ride rather easily. Heinken concluded by saying that for a moss to be transportable it must fragment and that this most probably occurs when the moss is dry, perhaps explaining the seasonal difference found for flying fox feces.

Hoofed Mammals

Larger animals contribute to dispersal in somewhat different ways. Their fur, hair, spaces between toes, feathers, and other parts can trap bryophyte parts and easily transport them for the distance travelled by the animal. Among these are large, hoofed mammals. Cattle and other farm animals are able to transport terrestrial taxa wedged in their hooves, causing certain bryophyte species to frequent cattle trails and ruts made by machinery (Crum 1973). The fur and hairs of hoofed mammals can provide a protective location for diaspores to hitch a ride and may take these diaspores for long distances (de Pablos & Peco 2007). Erika Péntzes-Kónya demonstrated the ability of overturned *Leucobryum juniperoideum* to form rhizoids on the overturned clump (Figure 123, Figure 133) after cattle traffic.



Figure 133. *Leucobryum juniperoideum* cushion with leaf rhizoids after overturn by cattle. Photo by Erika Péntzes-Kónya, with permission.

When Poschlod (pers. comm. 6 March 2013) applied diaspore traps in grasslands, he found many fewer vegetative parts than in peatlands. Rather, he found grazing animals, especially sheep, serving as long-distance dispersers of vegetative parts, especially from those moss species which do not form capsules (at least not in central Europe where he is familiar with the flora) such as *Abietinella abietina* (Figure 134). And this species is astonishingly widespread in all the dry calcareous (and man-made) grasslands there.



Figure 134. *Abietinella abietina* in Europe, a moss that is easily broken when dry, as it is here. Photo by Michael Lüth, with permission.

Several researchers have examined sheep and cattle coats (Figure 135) for propagules, primarily seeds, and found that greater seed weight was likely to prevent attachment on vertical surfaces but not on horizontal ones (de Pablos & Peco 2007). The same relationship is not likely to be a problem for the light-weight bryophyte diaspores. Sheep wool held more diaspores than the smoother coats of cattle. Both animals rest by lying down (Figure 136-Figure 137), providing ample opportunity for bryophyte adherence in rocky, mountainous pastures. In addition to clinging to the coats of hoofed mammals, the bryophytes can lodge on the hooves, particularly in the company of mud.



Figure 135. Sheep with full coat of wool before shearing in North Wales. At this stage, bryophyte fragments can easily adhere to the wool. Photo by Janice Glime.



Figure 136. Sheep resting under a tree near Swallow Falls, Wales. In areas where bryophytes are prevalent, this behavior contributes to attaching bryophyte fragments to the wool, facilitating dispersal. Photo courtesy of Kim Barton.

Sheep seem to be particularly good dispersal vectors, particularly those with a dense, curly fleece (Figure 135) (Pauliuk *et al.* 2011). The curly fleece is able to carry more fragments and larger species of bryophytes than those with smooth, fine hair (Figure 137-Figure 138). Twelve sheep representing two breeds were examined and revealed fragments from 16 species of mosses, representing 40% of the species present in the pasture. It is interesting that these were particularly common on the belly and tail! Some species disperse better than others, with pleurocarpous species, small species, and mats being over-represented compared to the pasture vegetation. On the other hand, large species, acrocarpous taxa, wefts, and turfs were under-represented among those cultured. The hooves transported mostly acrocarpous colonists. Short fragments were more likely to occur on the hooves; longer fragments were more common on the wool (Figure 139).



Figure 137. Sheep with closely sheared wool, creating a smooth surface to which bryophyte fragments don't adhere as well as they do to long, curly wool. Photo by Janice Glime.

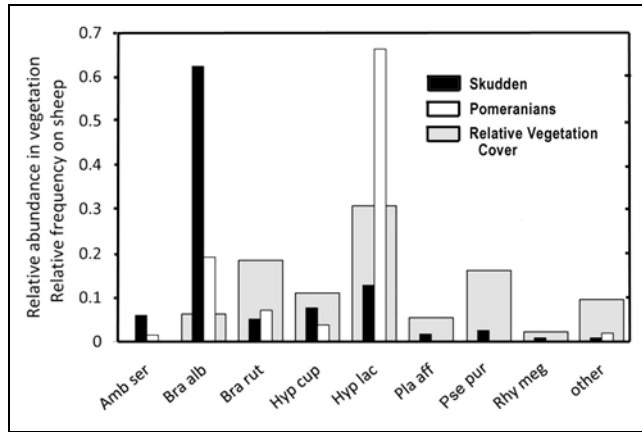


Figure 138. Comparison of proportions of bryophyte species carried by two different breeds of sheep, superimposed on the relative cover of the vegetation where the sheep were grazing. Skudden $n = 5,117$ fragments, Pomeranians $n = 7,2096$ fragments. Amb ser *Amblystegium serpens*, Bra alb *Brachythecium albicans*, Bra rut *B. rutabulum*, Hyp cup *Hypnum cupressiforme* var. *cupressiforme*, Hyp lac *H. cupressiforme* var. *lacunosum*, Pla aff *Plagiomnium affine*, Pse pur *Pseudoscleropodium purum*, Rhy meg *Rhynchostegium megapolitanum*. Modified from Pauliuk *et al.* 2011.

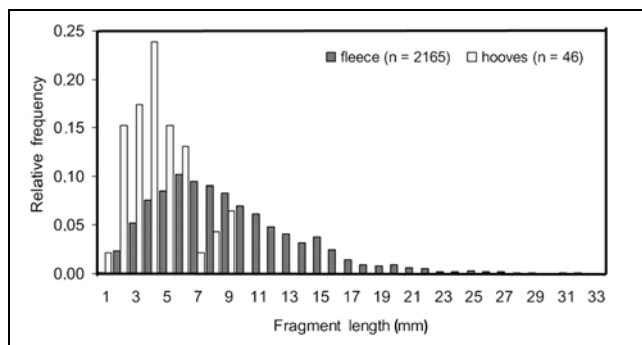


Figure 139. Size distribution of visible bryophyte fragments in fleeces and hooves from 12 sheep grazing on a dry grassland pasture. $n = 2206$. Modified from Pauliuk *et al.* 2011.

Heinken *et al.* (2001) further elucidated hoofed mammal dispersal by examining 25 shot roe deer (*Capreolus capreolus*; Figure 140) and 9 wild boar (*Sus scrofa*; Figure 141) in deciduous forests in Germany. They located a total of 106 bryophyte fragments (102 stem fragments, 4 leaves), representing 12 species, on the animals in their coats and hooves. This was proportionally somewhat less than the representation of tracheophytes based on percent cover (bryophyte:tracheophyte diaspores 1:30; bryophyte:tracheophyte cover 1:22.5).

Mean fragment length on the animals was 3.6 mm, but ranged 0.5-35 mm (Heinken *et al.* 2001). The fragments came mostly from the **terricolous** (on the soil) species, especially *Brachythecium velutinum* (Figure 142), *Hypnum cupressiforme* (Figure 143), *Eurhynchium hians* (Figure 125), and *Ceratodon purpureus* (Figure 126). Robust acrocarpous species in tall turfs were predominantly excluded, whereas the slender pleurocarpous species with erect, acute leaves, growing in wefts, were common. As in the dog study, some species that were frequent in the study area failed to adhere: *Atrichum undulatum* (Figure 132), *Plagiomnium affine* (Figure 144), *Pohlia nutans* (Figure

145), *Polytrichastrum formosum* (Figure 91). Others [*Brachythecium rutabulum* (Figure 146), *Mnium hornum* (Figure 90), and *Plagiomnium* sp.] only had a few fragments attached. The liverworts in the study area were completely absent on the animals, despite the scattered occurrence of *Chiloscyphus profundus* (= *Lophocolea heterophylla*; Figure 147) throughout the study area.



Figure 140. *Capreolus capreolus* (roe deer) male and female. Photo through Wikimedia Commons.



Figure 141. *Sus scrofa* (wild boar) in forest, lying among mosses. Photo by Rizzo, through Wikimedia Commons.



Figure 142. *Brachythecium velutinum* with capsules in southern Europe. Photo by Michael Lüth, with permission.



Figure 143. *Hypnum cupressiforme*, a species whose fragments commonly appeared on a dog in a German dispersal experiment. Photo by Dick Haaksma, with permission.



Figure 144. *Plagiomnium affine*, a species that failed to adhere to a dog in a German dispersal experiment. Photo by Michael Lüth, with permission.



Figure 145. *Pohlia nutans*, a species that failed to adhere to a dog in a German dispersal experiment. Photo by Michael Lüth, with permission.



Figure 146. *Brachythecium rutabulum* (Rough-stalked Feather-moss), a moss that is uncommon among the fragments on a dog in a German dispersal experiment. Photo by Barry Stewart, with permission.



Figure 147. *Chiloscypus profundus* (= *Lophocolea heterophylla*), a liverwort that does not seem able to hitch-hike a ride on roe deer or wild boar. Photo by Michael Lüth, with permission.

Heinken and coworkers (2001) tested the ability to pick up bryophyte fragments by experimenting with a dummy deer. This dummy was placed on its stomach on the forest floor and used to mimic wallowing by giving it a gentle rolling motion. They repeated the experiment 300 times between July and October, cleaning all adhering fragments each time. This "behavior" produced 51 bryophyte fragment hitchhikers. Four of the six terricolous bryophyte species in the sample plots adhered to the ventral hair, with strong differences among bryophyte species. *Eurhynchium hians* (slender with erect, acute leaves, forming wefts; Figure 125) had 47 adhering stem fragments, whereas the similarly dominant *Plagiomnium undulatum* (robust with rounded leaves, forming tall turfs; Figure 148) had only one adhering fragment.



Figure 148. *Plagiomnium undulatum*, showing its large, rounded leaves that do not adhere easily to fur. Photo by Des Callaghan, with permission.

Heinken *et al.* (2001) concluded that most of the attachment to fur occurs when the animals lie down or wallow on the ground, or when they rub against rocks, walls, or tree trunks. The hooves can also transport fragments, particularly in adhering mud (Figure 149). The type of fur matters. The boar provides further advantages by its frequent rooting and wallowing, extensive resting periods, and difficulties with grooming. Even their feces (Figure 150) could carry diaspores, but we don't know if they will survive. Since wild boars can travel as much as 5 km per day through the European forests, they could facilitate transport for quite some distance.



Figure 149. *Sus scrofa* (wild boar) tracks showing the mud that is a common part of the boar's environment. Mud on the hooves can help to carry bryophyte diaspores. Photo by James K. Lindsey, with permission.



Figure 150. *Sus scrofa* (wild boar) scat, a potential but untested means of dispersal. Photo by James K. Lindsey, with permission.

Pérez (2010) considered goats as contributors to dislodging mosses, particularly *Grimmia trichophylla* (Figure 151) and *G. torquata* (Figure 152) on Haleakala's Crater, Maui, Hawai'i, USA. These were transported downslope to new locations where they could grow, perhaps a combination of fragmentation by goats and gravity.



Figure 151. *Grimmia trichophylla* on rock. This moss may be dislodged by goats on Maui, Hawaii, and subsequently roll down the slope, making moss balls. Photo by Michael Lüth, with permission.



Figure 152. *Grimmia torquata* on rock. This moss may be dislodged by goats on Maui, Hawaii, and subsequently roll down the slope, making moss balls. Photo by Michael Lüth, with permission.

Bears

When I was searching for images of bears in streams, I found one with a group of bears in a moss-laden tree in the temperate rainforest of Canada (Figure 153). It occurred to me that these bears, and most likely monkeys, big cats, and other climbers, would dislodge some of the bryophytes, hence facilitating their dispersal. Another image of a black bear climbing over a rock with a vascular plant draped around its head suggested that especially for pendent mosses, they could carry them away, perhaps for some distance, and if the bryophyte is lucky, it might even be deposited in another tree.



Figure 153. *Ursus americanus* among pendent mosses in Tongass National Forest. Photo by Interpretive staff, Tongass National Forest, Alaska, USA, through public domain.

In addition to dispersal of plants on the fur, bears may also disperse them through feces. Wilson and Ruff (1999) report that mosses are included among the food, but we have no information on the viability of mosses that pass through the digestive tract of the bear.

Bryophyte vegetative structures generally are not adapted for animal dispersal. Nevertheless, just by their location they are likely to be carried on amphibian skin, turtle carapaces, slug slime, insect guts and surfaces, hairs of mites and spiders, stuck to feathers and beaks of ducks, and on animal hooves and fur. Nest-building birds that line their nests with mosses often drop pieces, or the moss can even grow while within the nest. It appears that most vegetative parts do not survive the guts of most animals well, but some do and can thus be carried to new locations.

Human Dispersal

Humans are often inadvertent dispersal agents. For example, van Zanten and Pócs (1981) report on fragmentation of mosses by lawn mowers. These are then carried further by the lawn mower or by the human raking up the scraps. Others are torn apart during logging operations, adhering to the equipment, and potentially

being carried many kilometers to another site. And certainly back packs and collecting bags carry small scraps of bryophytes that escape the fate of a herbarium packet. Van Zanten and Pócs (1981) noted that when they walked in a dry meadow in New Zealand, their socks became transport agents of fragments of *Thuidiopsis furfurosa* (Figure 154). This suggests that other animals could likewise transport this species on fur or feathers.

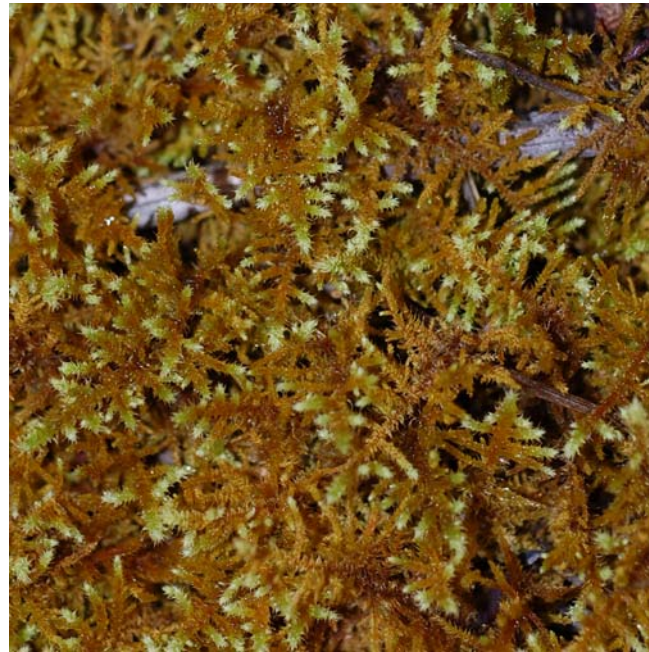


Figure 154. *Thuidiopsis furfurosa*, a species that is known to cling to socks of bryologists. Photo by David Tng, with permission.

Bryum argenteum (Figure 27) is commonly dispersed by humans. It has deciduous shoot apices that apparently attach to shoes and other clothing as well as to small animals. It is common along paths in cemeteries, around tennis courts, and in golf courses. Clare and Terry (1960) used matchbooks in an elegantly simple experiment to demonstrate dispersal in this species. They "walked" the matchbook across patches of *B. argenteum*, then across soil. As a control, they walked matchbooks that had not contacted *B. argenteum* across other patches of soil. The *B. argenteum* became established on the plots where the matchbook had previously visited the mosses, but not on the others, demonstrating how easily it could be dispersed on shoes and feet.

There are several documented cases of bryophytes dispersed by humans. One of the most recent reports is that of Ireland and Shchepanek (1993) for the spread of *Hyophila involuta* (Figure 155) in Canada. This species was known only from a few localities in Ontario. However, it is growing abundantly on the sides of most of the locks in the Rideau Canal and the authors suspect that it arrived in both Michigan and Canada from more southern localities by travelling there on boats. The locks are constructed of limestone and sandstone or concrete, and the plants seem to get started along the mortar seams.



Figure 155. Gametophytes of *Hyophila involuta* growing on concrete. Photo by Michael Lüth, with permission.

I still recall Iwatsuki commenting in Japan that he didn't need to check what was growing on the concrete retaining walls along the roads – it was all *Hyophila* (Figure 155). However, on the locks in Ontario it is nearly devoid on the concrete blocks, occurring predominately on the limestone and sandstone blocks which are more similar to the construct in Japan (Ireland & Shchepanek 1993). In the Ontario locks, it grows only below the water level, sometimes even on the bottom of the locks. Frequent wetting and drying and low light intensity seem to favor its growth, but the plants must also survive seven months out of the water in winter when the locks are drained. These plants never have sporophytes, and with only one report of sporophytes in the United States, it appears that they rely on their numerous multicellular gemmae (Figure 156).



Figure 156. *Hyophila involuta* showing numerous gemmae that form at leaf bases. Photo by Michael Lüth, with permission.

Logging vehicles, all-terrain vehicles, and other forest transport have giant tires with the potential to pick up fragments of bryophytes along with soil. Some of these could travel considerable distances to another location before falling off. It appears that hitch hiking is a common mode of travel for *Riccia* – in Michigan, USA, *R. huebeneriana* (Figure 157) and *R. cavernosa* (Figure 158) are often dwellers along disturbed soil of 2-track roads, suggesting a vehicular means of dispersal (Crum 1973).

Horticulture provides several means of introducing species to new locations. *Marchantia polymorpha* (Figure 32) is frequently spread throughout a greenhouse by the force of the watering system. This and other bryophytes then travel in the pots with the purchaser. *Polytrichastrum longisetum* (Figure 159) is an introduced horticultural weed in West Cornwall, Great Britain (Holyoak 1995).



Figure 157. *Riccia huebeneriana*, a common liverwort along two-track roads. Photo by Des Callaghan, with permission.

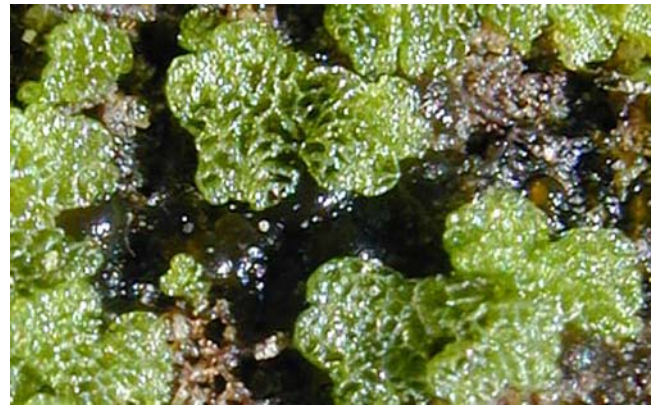


Figure 158. Thalli of *Riccia cavernosa* on disturbed soil. Photo by Michael Lüth, with permission.



Figure 159. *Polytrichastrum longisetum*, an introduced horticultural weed in West Cornwall, Great Britain. Photo by Michael Lüth, with permission.

Bryophytes used as packing material are potential propagules. Degener *et al.* (1969) reported such dispersal to explain the "unnatural distribution" of *Sphagnum palustre* (Figure 160). Its appearance in Hawaii seems to be from use of this moss as packing material for tree seedlings. Bryophytes used for packing can escape and become established, as in the case of *Pseudoscleropodium purum* (Figure 161), in widely ranging parts of the world (Allen & Crosby 1987).



Figure 160. *Sphagnum palustre*, a moss that is spread by its use in packing tree seedlings. Photo by Michael Lüth, with permission.



Figure 161. Gametophyte of *Pseudoscleropodium purum*, a widely transported packing material. Photo by Michael Lüth, with permission.

Golf courses and picnic areas seem to be common sites for invasive species because they get considerable foot traffic from a wide range of locations. The first citing of *Fissidens taxifolius* (Figure 75) in Auckland, New Zealand, was reported occurring under a picnic table (Espie 1997). Also *Rhytidiadelphus squarrosus* (Figure 131) first appeared in New Zealand on a Dunedin golf course in 1975, presumably arriving with foot traffic, or perhaps a golf bag.

Paths are often bordered by bryophytes (Figure 162- Figure 163). Such is the case in the Tatra Mountains of the Western Carpathians where one can find 15% of the liverwort species of that area (Górski 2009). Górski refers to "walking down" of high mountain species [*Marsupella brevissima* (Figure 164), *Pseudolophozia sudetica* (Figure 167)] to lower sites, "passing" of alpine scree-bed species to habitats associated with humans [*Anthelia juratzkana* (Figure 168), *Marsupella brevissima*, *Pleurocladula albescens* (Figure 169)], and formation of new combinations of plant communities [with *Cephalozia bicuspidata* (Figure 165)] or expansion of communities already associated with human activity [e.g. *Calypogeietum trichomanis*, *Nardietum scalaris* (Figure 166)]. Although there is no proof or experimentation to support this, it is likely that at least some of these have arrived in these locations due to human dispersal on foot gear. Others are simply opportunists that are able to

occupy a suitable habitat created by humans, possibly facilitated in their dispersal by the openings created by the paths.



Figure 162. Mosses along forest trail at Clear Creek Park in Ohio, USA. The trail opens new habitats on the slopes and foot traffic can bring propagules to the scene. Photo by Janice Glime.



Figure 163. Mosses at edge of a blacktop path at Three Creeks Park, Ohio, USA. These are easily fragmented by human foot traffic, creating dispersal potential. Photo by Janice Glime.



Figure 164. *Marsupella brevissima*, a leafy liverwort that gets "walked down" the mountain along paths. Photo by Jan-Peter Frahm, with permission.



Figure 165. *Cephaloziella bicuspidata*, a species subject to new community combinations due to "walking down" of alpine species. Photo from Botany Website, UBC, with permission.



Figure 166. *Nardia scalaris*, primary species in the *Nardietum scalaris*. Photo by J. C. Schou, with permission.



Figure 167. *Pseudolophozia sudetica*, a leafy liverwort that gets "walked down" the mountain along paths. Photo by Jan-Peter Frahm, with permission.



Figure 168. *Anthelia juratzkana*, a scree-bed species that gets transferred to human habitats. Photo by Michael Lüth, with permission.



Figure 169. *Pleuroclada albescens*, a scree-bed species that gets transferred to human habitats. Photo by Michael Lüth, with permission.

Bryophytes may even be transported deliberately. My favorite story is one in which *Fontinalis antipyretica* (Figure 20) was introduced into South Africa in an attempt to encourage more aquatic insects as food for fish (Richards 1947). The moss spread rapidly and covered the rocks. But at least initially, the attempt to improve the aquatic insect population failed because the native species were adapted to smooth rocks and they in fact lost their habitat.

Despite the role of humans in dispersal, urban areas often exhibit depauperate bryophyte floras. One of the reasons for this is the fragmented nature of the urban landscape, making dispersal difficult (Korpelainen *et al.* 2006), especially for epiphytes. Of course, the inhospitable nature of the urban habitat, especially exposure, makes establishment difficult once a diaspore arrives.

Mystery Dispersal

Most bryophyte dispersal is in fact mystery dispersal. Few species have actually been subjected to experimentation, tagging, or other means to provide scientific data on their dispersal. Dickson *et al.* (pers comm. 23 April 2013) have provided me with one such

story for *Fissidens fontanus* (Figure 170) in France. This species occurs in many of the abandoned lavoirs that still have flowing clean water; abandoned in the 1960s, the lavoirs were communal wash houses where women did family laundry. They were mainly constructed in the nineteenth century and some villages had more than one. These usually have a roof, but they are open on one or more sides and accessible to birds and insects (and probably an occasional frog). They have become inhabited by algae and bryophytes, the moss *Fissidens fontanus* (Figure 171). No capsules are known for this species in Europe. Recent searches of lavoirs have revealed more locations (Piguet *et al.* 2007; Piguet 2009), and it seems to be increasing along rivers in Germany and perhaps in France. Dickson and colleagues raise the question of its dispersal. There are no known connections among the springs that feed them and no ducks have been seen at any of the lavoirs. How does it spread between lavoirs – I'm guessing it was animals.



Figure 170. *Fissidens fontanus*, a moss that has appeared in lavoirs in France. Photo by Michael Lüth, with permission.



Figure 171. *Fissidens fontanus* in lavoir at Vouchoux, France. Photo courtesy of James Dickson.

Invasive Species

Invasive species represent the epitome of dispersal. Often it is the human species that serves as the dispersal vector. But whatever the vector, these species are good at getting there and successful at establishment.

One of the best known of the invasive bryophyte species is *Campylopus introflexus* (Figure 172) (Fudali 1992; Schirmel & Buchholz 2013). This species is responsible for altering the invertebrate communities in the acidic coastal dunes of Europe where it is able to form dense carpets. It caused changes in both body size and feeding preference among the arthropods, resulting in changes in hunting mode of spiders. Spiders increased in functional diversity, whereas carabid beetles had a reduction in functional diversity.

Another well-known invasive species is *Orthodontium lineare* (Figure 173) (Herben 1994). The key to success for this species is that it seems to be able to grow on whatever substrate is available, being limited only by available space.



Figure 172. *Campylopus introflexus*, an invasive species in Europe and parts of North America. Photo by Janice Glime.



Figure 173. *Orthodontium lineare*, an invasive species in Europe. Photo by David T. Holyoak, with permission.

Essl *et al.* (2013) assessed bryophyte invasions and what makes them work, using 82 regions spanning five continents as their data sources. They identified 139 species (106 mosses, 28 liverworts, 5 hornworts) that they

considered to be alien in at least one study region. They found that alien numbers were significantly higher on islands than on the studied continental regions. They identified 34 species as accidental hitch-hikers and 27 species as accompanying ornamental plants. These invasive species prefer strongly disturbed habitats [ruderal vegetation (growing on waste ground), roadsides, lawns], whereas forests and rocks are typically avoided. They concluded that the pattern of bryophyte invasions is different from that of tracheophytes.

Summary

Dispersal methods of vegetative diaspores of bryophytes include gravity, wind, water, and animals. Although most bryophytes are suitable for wind dispersal, even for fragments and specialized propagules, gravity accounts for the short distances to which most of these vegetative diaspores travel.

Splash cups are useful in dispersing gemmae in several liverworts and one family of mosses. Bryophytes getting frozen in ice or caught by flood waters can be carried considerable distances and vegetative dispersal in flowing water environs is essentially guaranteed.

Animal dispersal is probably more important than has been presumed, and includes earthworms, arthropods (insects, mites, pillbugs, spiders, harvestmen), slugs, amphibians, turtles, water birds, nest-building birds, and animal feet and fur. Birds and rodents often dislodge bryophytes while searching for food items among them and may carry fragments among their feathers/fur or attached to feet. Humans disperse bryophytes through their own footwear, vehicle tires, horticulture, and packing materials. However, none of the bryophyte vegetative propagules seems to be especially adapted for animal dispersal.

Although most bryophytes are best adapted to wind dispersal, even of fragments and specialized propagules, gravity accounts for the short distances to which most of these vegetative structures travel.

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CHAPTER 4-12

ADAPTIVE STRATEGIES: SPECULATION ON GAMETOPHYTE STRUCTURES

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CHAPTER 4-12

ADAPTIVE STRATEGIES: SPECULATIONS ON GAMETOPHYTE STRUCTURES

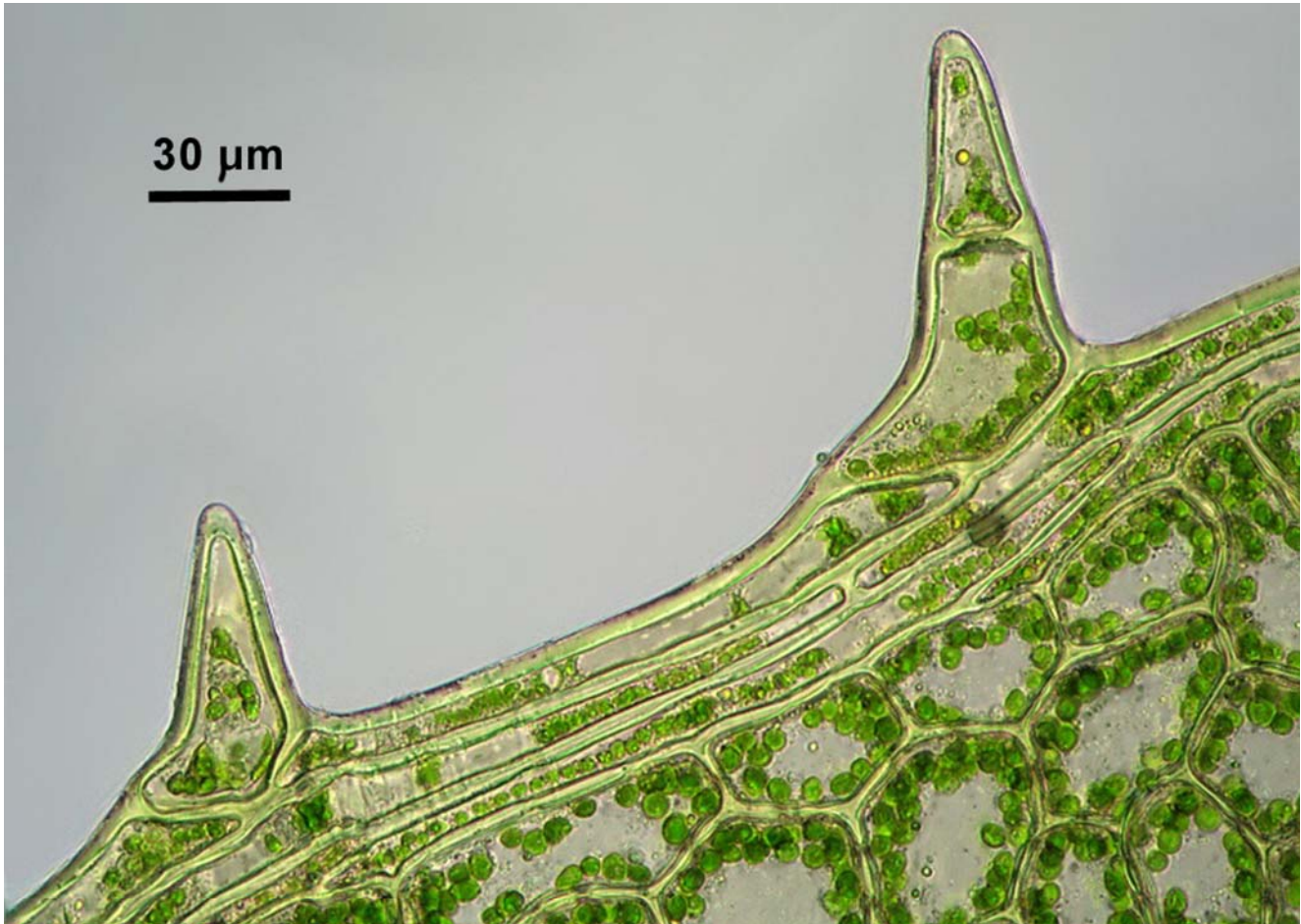


Figure 1. *Plagiomnium affine* leaf border with teeth. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

Prologue

As I begin this chapter, I am reminded of a conversation I had with Louis Anderson. It was similar to the one relayed by Brent Mishler on Bryonet (8 May 2012) on the position of Lewis Anderson. When asked about the function of something like a hairy surface, he would point out that it had to have some kind of surface. We must keep this admonition in our minds constantly as we question functions of bryophyte parts, forcing us to ask more precise questions and to **test** our hypotheses.

Not all structures have adaptive value. With this caution in mind, we need to be aware if something is really adaptive or it is simply not an encumbrance. If it persists through more than one taxonomic group, is it more likely it has some adaptive significance than if its presence is rare? And if it occurs in all, might it be a necessity? But I dare not go farther in defining adaptive value. Hence, this

chapter is necessarily speculative. Do keep that in mind as you read.

The descriptions of structural adaptations are largely the product of the human mind to seek explanations for things. Hence, we seek to learn why a certain structure persists in a bryophyte by trying to find a function for that structure. This teleological approach is not all bad. It can form the basis of our alternative hypotheses, the null hypothesis being that there is no special function.

The next step after identifying a hypothesis is attempting to test it, and this is often quite difficult. It often becomes necessary to ask the question, "What would happen if this structure were absent, as for example the teeth shown in Figure 1?" Modern genetic techniques are permitting us to identify the functions of genes that way, using knock-out genes to disable or remove a gene. Some

structures are suitable for removing or disabling as well and can help us test our hypotheses.

Even with such testing, we must also keep in mind that not all structures have functions, and that structures and genes may not work alone. For selection to work against them, there must be some cost for their presence. If there is no cost, a structure may remain, seemingly with no purpose.

Often this cost is expenditure of energy, whereas when we look for adaptive value we tend to look for things like moisture conservation, herbivory protection, or increased dispersal. All of these relate to survival, so testing of adaptations often is a testing of survival value.

In this regard, we need to consider that Lamarckian evolution suggested that giraffes have long necks so they could reach higher branches where there was less competition for food. But there is no genetic mechanism that can cause a gene to arise due to need. Genes arise randomly through mutations or get lost through deletions. Combinations of genes change due to both mutations and recombinations. The recombinations can occur through mixing in meiosis or through mating with an individual with genotypic differences.

Linked Genes

A second complicating factor in our search for function is that genes may be kept because of their nearness to another important gene. If gene B resides on a chromosome with gene A, it will go where gene A goes unless it gets moved during a crossover event (a common occurrence during meiosis) or other type of rearrangement. The closer it is to gene A, the lower the chances of gene B becoming separated during a crossover event. If gene A is an important adaptive gene, and gene B does little or no harm, then it will be kept as it travels along with gene A, even if it codes for something that offers no adaptive value. But if gene B is harmful, and gene A is not essential or is unable to provide more benefit than the harm caused by gene B, then gene B will begin to disappear from the gene pool – and gene A with it. I could explain this further, but you should be able to see my point – not all structures or physiological mechanisms are necessarily advantageous. They may be non-adaptive. They may even remain from a time when they were adaptive to conditions that no longer exist. Thus, we must keep in mind that not all structures or other phenotypic expressions are adaptive. The evolutionary model would, in fact, predict that some are not adaptive. And those that are maladaptive may take hundreds of years or even eons to disappear from the population. In the meantime, they may offer us taxonomic characters that are useful to systematists!

It is not easy to associate a given character with a particular gene. Vanderpoorten and Jacquemart (2004) found that most of the morphological variation in the aquatic moss genus *Amblystegium* (*Hygroamblystegium*; Figure 2) result not from genetic differences, but in plasticity of expression. They also found that the evolution of most characters in these aquatic taxa was often independent from phylogeny of the taxon. Rather, the morphological characters in this genus lack independence and stability, making them less useful for distinguishing species.



Figure 2. *Hygroamblystegium fluviatile*. Photo by Hermann Schachner, through Creative Commons.

Evolutionary Drivers

Kürschner (2004) found common adaptive trends among the bryophytes from the Near and Middle East. These represented independent traits that arose in unrelated taxa evolving under similar habitat conditions. Such convergence suggests relationships of evolution with site ecology and niche differentiation.

Hence, this chapter will present more hypotheses than facts with the challenge to our young (and older) bryologists to test these.

GAMETOPHYTE

Schofield (1981) reviewed the literature and concluded that spore germination patterns, protonemal structure, life span, and methods of vegetative propagation are all related to nature of the habitat. Large, multicellular spores and swollen protonemal cells are more common in habitats that frequently experience desiccation. Protonemata are more specialized in deeply shaded environments. More typical types with strongly elongate cells are more frequent in mesic sites or terrestrial sites with favorable moisture conditions during at least part of the day during most of the growing season. Growth forms may be correlated genetically, or they may be "molded" by the environment. Energy conservation is often accomplished by having production of gemmae at different times from sexual reproduction.

In **ectohydric** (external) conduction systems, water movement is facilitated by leaf shape, arrangement, orientation (Figure 3), and detailed anatomy; branch arrangement, stem cortical cells; and the presence of rhizoids or paraphyllia (Schofield 1981). Surface ornamentation of leaves, stems, and rhizoids also may contribute. In **endohydric** (internal; Figure 12-Figure 13) conduction, the hydrome and leptome facilitate water movement and may be habitat specific, especially in the **Polytrichidae**. Again, there is little experimental evidence to support the conclusions that currently rest on habitat correlations.



Figure 3. *Pohlia* sp. with raindrops large and small, illustrating the way ectohydric water becomes trapped in the leaf axils. Photo by John Game, through Creative Commons.

Wetlands vs Non-wetland Trends

Hedenäs (2001) took compiled data that supports much of the tendencies noted by Schofield (1981) by examining frequencies of 86 character states in 439 species of pleurocarpous mosses on a worldwide scale. These were compared across climatic zones, general habitat, and wetland to non-wetland gradient. He found that 44% of the characters are indeed influenced by climatic zone – the largest sphere of influence in the study. General habitat accounted for 35% and wetland to non-wetland gradient 23%.

In the Hedenäs (2001) study, two complex functions emerged. Water conduction and retention can be measured by differences in stem central strand morphology, leaf orientation, leaf costa type, alar cells, paraphyllia, pseudoparaphyllia, inner perichaetial leaf plications, vaginular paraphyses, capsule stomatal pore, operculum type, and possibly seta length. The second important function is spore dispersal, facilitated by capsule shape and orientation, annulus, exostome and endostome appearance, spore size and maturation time, and possibly seta length. the importance of phylogenetic history cannot be ignored as a limiting factor on adaptive characters, but other drivers include water availability and exposure to wind.

As seen in Chapter 2, bryophytes have a leafy **gametophyte** generation with one set of chromosomes (**haploid**) and a **sporophyte** generation that produces a capsule atop a short or long stalk and having two sets of chromosomes (**diploid**). The morphology of these two generations is strikingly different, so it is expedient to divide our discussion into these two generations.

Proctor (2010), a very astute bryologist who is familiar with both bryophyte physiology and structure, has summarized his perspective, supported by literature, on bryophyte adaptations.

Without considering how traits got that way, or which bryophytes are their ancestors, let us consider the traits themselves and their possible adaptive roles. Proctor (2010) compares the wide diversity of leaf shape, proportions of costa (see below under Costae) and lamina, and cell shape (Figure 4) in the **Dicranaceae** to the essentially uniform structure of the ecologically diverse **Fissidentaceae** (Figure 5; Figure 82). Such comparisons testify to the complexity of such adaptive considerations.

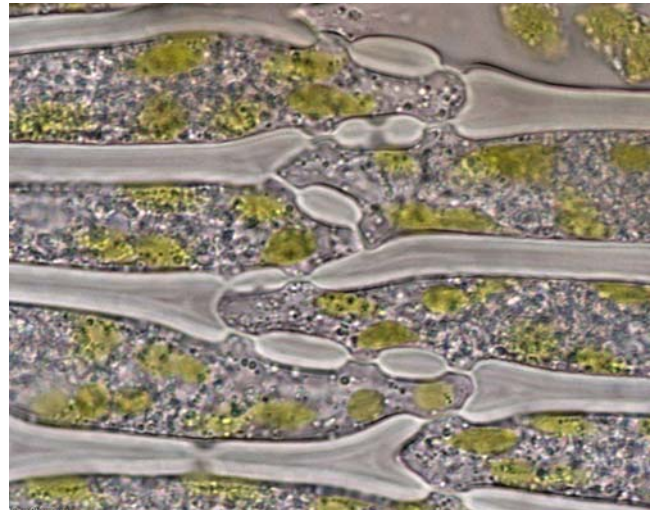


Figure 4. *Dicranum polysetum* leaf cells showing porose walls. Photo by Walter Obermayer, with permission.



Figure 5. *Fissidens rivularis*, showing the costa, 2-ranked leaves, and flattened appearance that are present in all members of the genus. Photo by Des Callaghan, with permission.

Other families seem to have structures that adapt the family to narrower environmental circumstances. For example, the **Orthotrichaceae** live in the xeric locations of rocks and tree bark, supported by desiccation tolerance, cushion growth forms (Figure 6), and small isodiametric leaf cells (Figure 7), all of which help them to survive drying. **Hookeriaceae**, by contrast, have large, thin-walled cells (Figure 8-Figure 9) and survive only in moist, shady locations (Figure 10).



Figure 6. *Orthotrichum obtusifolium* forming a cushion on a tree trunk. Photo by Michael Lüth, with permission.



Figure 7. *Orthotrichum pusillum* showing isodiametric leaf cells. Photo by Bob Klips, with permission.



Figure 8. *Hookeria lucens* leaf showing thin-walled cells. Photo by Malcolm Storey <www.discoverlife.org>, through Creative Commons.

Stem

The bryophyte stem offers both support and a way of scavenging into a wider space. Pleurocarpous mosses extend across the ground surface, taking advantage of the sunflecks on part of the moss while other parts are in the shade, a phenomenon that has been termed **foraging**

(Figure 11). In some mosses, a central strand with specialized elongated **hydroids** and **leptoids** (Figure 12- Figure 13) contribute to transport of water, nutrients, and other substances, whereas in others these must travel from unspecialized cell to cell. Are there habitat conditions when ordinary cells are a better means of providing transport?

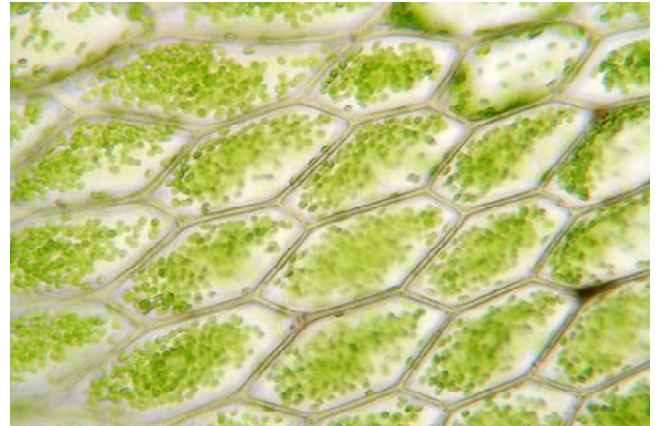


Figure 9. *Hookeria lucens* thin-walled leaf cells. Photo by Malcolm Storey <www.discoverlife.org>, through Creative Commons.



Figure 10. *Hookeria lucens* near Swallow Falls, Wales, where this whitish moss is kept moist by other mosses on a damp log in a stream valley. Photo by Janice Glime.



Figure 11. *Brachythecium buchananii* partly in sun and partly in shade. Connected plant parts can transfer photosynthate, and nutrients, from one part to the other through **foraging**. Photo by Michael Lüth, with permission.



Figure 12. *Bryoxiphium* stem ls showing long hydroids (green on left) and leptoids (reddish brown) compared to ordinary cortex cells (green or right). Photo courtesy of Izawa Kawai.

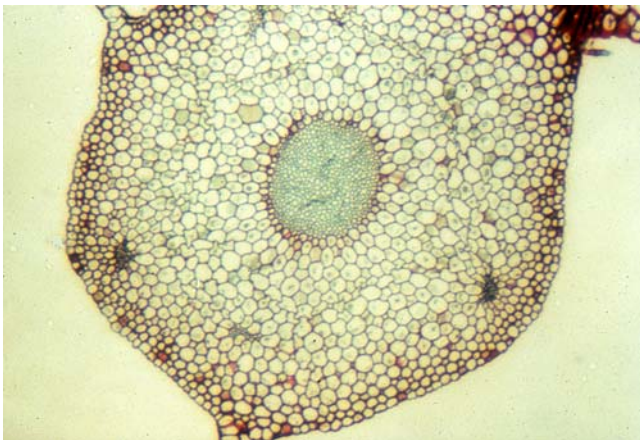


Figure 13. Stem cross section of the moss *Mnium*. Blue-stained cells in center are **hydroids**; red-stained cells immediately around them are **leptoids**. Photo by Janice Glime.

Richard Zander (Bryonet 8 May 2012) suggested that it might help to demonstrate a biophysical principle when one is unable to demonstrate an adaptation experimentally. As an example, he suggests that the cross section of a stem of *Aloina hamulus* (Figure 14) shows no central strand or sclerodermis. Rather, only a crowded set of cells is present. Zander compares that crowded set (see *e.g.* Figure 15) to the crowded bubbles of soap froth (Figure 16). And soap films assume the least area or least distance solution to their arrangement. He suggests that a stem with

this arrangement therefore uses the least amount of photosynthate to create a plant axis. This would seem to be the simplest unspecialized case.



Figure 14. *Aloina hamulus*, a xerophytic moss with no central strand in its stem. Photo by Claudio Delgadillo Moya, with permission.

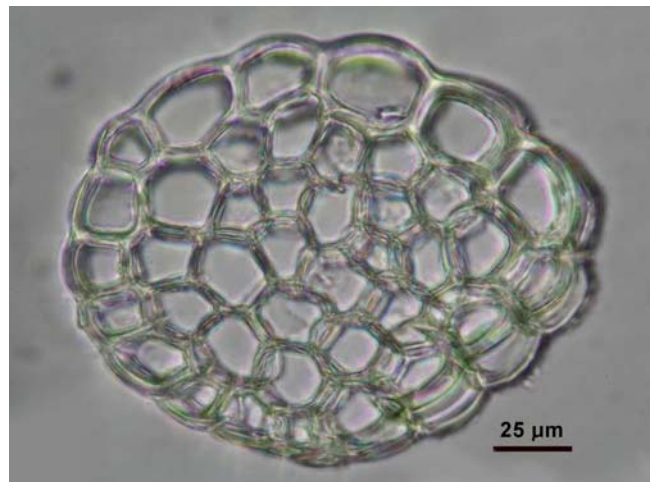


Figure 15. Leafy liverwort *Telaranea pallescens* stem cross section showing the "bubble" arrangement of cells described by Richard Zander. Photo by Tom Thekathyl, with permission.



Figure 16. Soap bubble arrangement maximizing contact. Note pyramidal cells at the corners – reminiscent of trigones. Photo by Janice Glime.

Stem Structure

Stems are usually circular (Figure 17), but some are triangular in cross section (Figure 18); others are somewhat

flattened (Figure 19). They can have layers of cells that differ in wall thickness and coloration. Some of these differences are expressed by cells in the central strand (Figure 17-Figure 18, Figure 22-Figure 23), but not all bryophytes have a central strand (Figure 15, Figure 19-Figure 21). Others are expressed in the outer cells and can contribute to reduction in water loss and strengthening of stems. But little testing has been done to determine how these outer cells really help. Are they hydrophobic? Do any help in the absorption of water? Do the strengthening cells correlate with habitats where stem strength is an advantage? Do the colors and thickness of the outer layer respond to the environment?

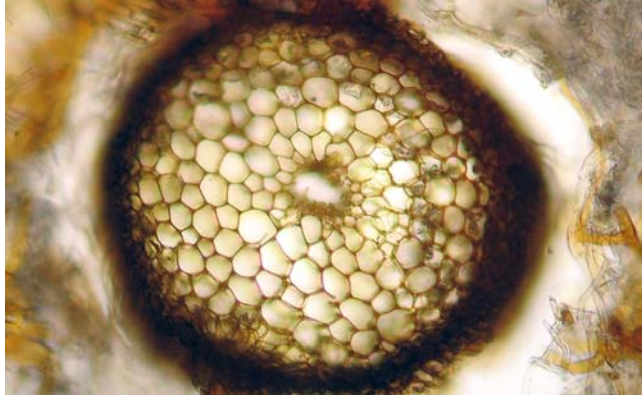


Figure 17. *Dicranum scoparium* stem cross section with outer cells having thick, darkly colored walls, thin-walled cortical cells, and rudimentary central strand. Photo from Botany Department website, University of British Columbia, BC, Canada, with permission.

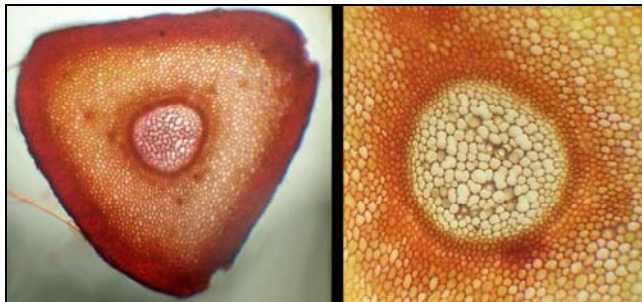


Figure 18. *Dendroligotrichum dendroides* stem cross section showing triangular shape. Image on right shows details of the central strand. Photo by Juan Larrain, with permission.

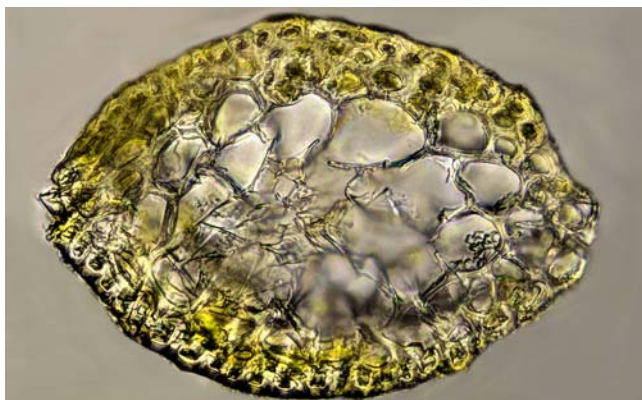


Figure 19. *Fissidens bryoides* stem cross section showing thick-walled outer cells and thin-walled central cells with no central strand. Photo by Dick Haaksma, with permission.

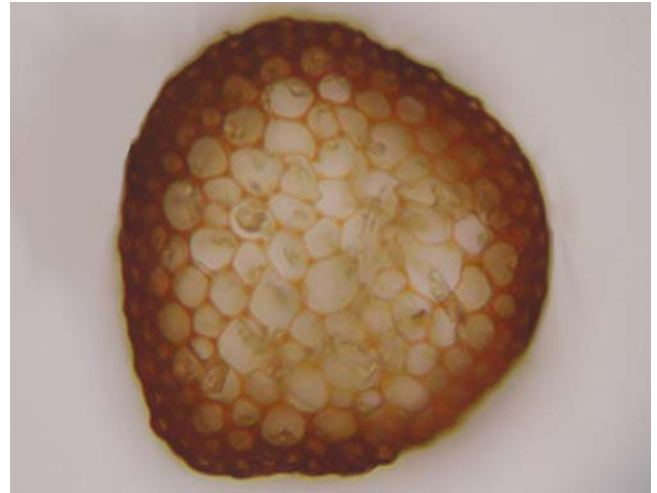


Figure 20. *Andreaea* stem with no central strand but with color in all the cell walls, suggesting phenolic pigments. Photo from Botany Department website, University of British Columbia, BC, Canada, with permission.



Figure 21. *Hylocomium splendens* stem cross section showing thick-walled, colored outer cells and thin-walled cortex with no central strand. Photo from Botany Department website, University of British Columbia, BC, Canada, with permission.

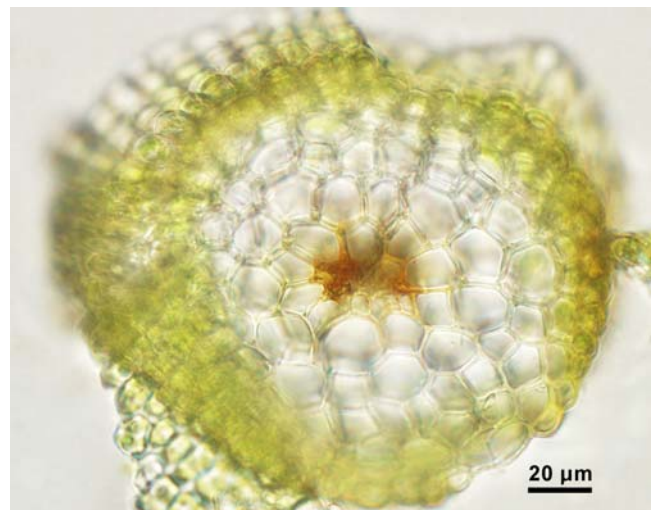


Figure 22. *Molendoo sendtneriana* stem cross section showing outer photosynthetic cells, translucent cortex, and central strand. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.



Figure 23. *Polytrichastrum formosum* stem cross section showing thick-wall, colored outer cells, colored walls of cortex cells, thin-walled leptoids (food-conducting cells) and thick-walled, colored hydroid cells, the latter two cell groups forming the central strand. Photo from Botany Department website, University of British Columbia, BC, Canada, with permission.

Several studies have addressed the thickness of the stem and the thickness of the outer layer under different environmental influences. See and Glime (1984) compared the stem thickness and stem wall thickness in *Fontinalis flaccida* (quiet water; Figure 24-Figure 25) and *F. dalecarlica* (fast water; Figure 26-Figure 27) after growing them in a common garden artificial stream. The new growth on both species retained their distinctness, with *F. dalecarlica* having both thicker stems and more thickened outer cells (Figure 28). Furthermore, even the central cortex cells of *F. dalecarlica* were thickened, whereas they were not in *F. flaccida*.



Figure 24. *Fontinalis flaccida* showing thin stems for this quiet-water species. Photo by Lance Biechele, permission pending.

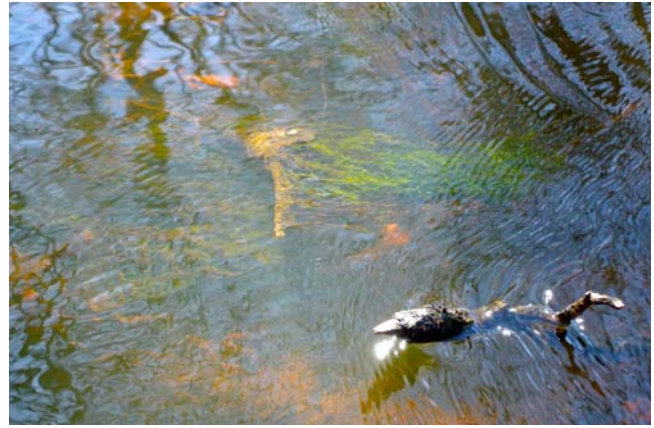


Figure 25. *Fontinalis flaccida* in relatively quiet stream water. Photo by Lance Biechele, permission pending.

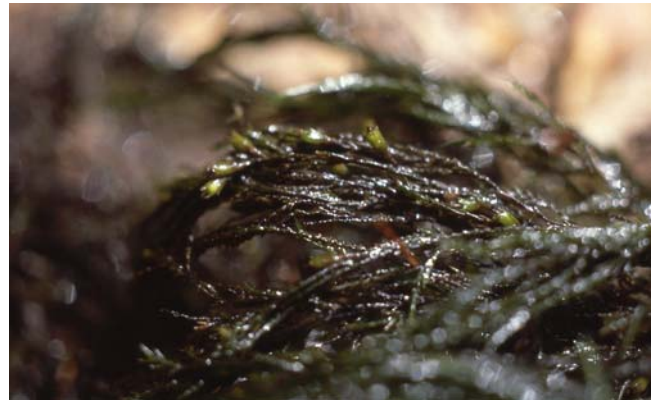


Figure 26. *Fontinalis dalecarlica* showing thick, strong stems. Photo by Janice Glime.



Figure 27. *Fontinalis dalecarlica* in a fast mountain stream. Photo by Janice Glime.

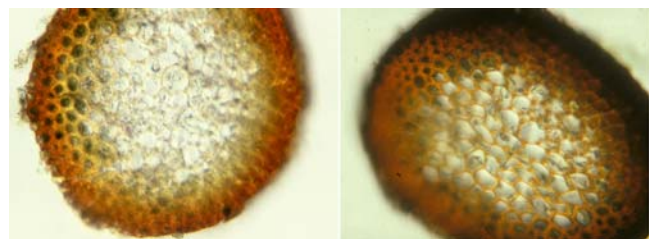


Figure 28. *Fontinalis flaccida* (left) and *F. dalecarlica* (right) stem cross sections showing the thickened (and colored) cortex cells and thicker outer layer of *F. dalecarlica* (right). Photos by Janice Glime.

Li *et al.* (1992) found that stem width in two *Sphagnum* species was plastic and differed significantly within species between those grown in water and those grown above water (Figure 29). Those above water developed 1-2 additional rows of hyaline cells in the outer layer of the stem (Figure 30). It is interesting that the less drought-resistant *S. papillosum* (Figure 31) had the greater difference in stem width between the two conditions. Despite that difference, *Sphagnum magellanicum* (Figure 32) is better at moving water than is *S. papillosum* and when grown in mixed clumps or alone it remains wet longer, whereas *S. papillosum* dries out quickly when it is in a hummock alone, but retains water as long as *S. magellanicum* when it grows mixed with it in about equal numbers (see Chapter 7-3).

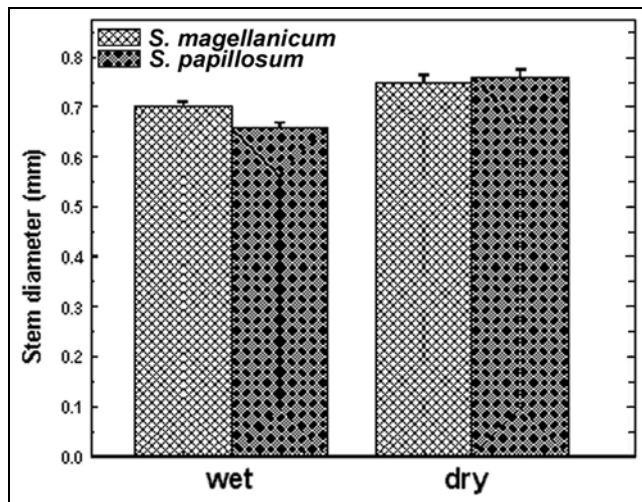


Figure 29. *Sphagnum magellanicum* and *S. papillosum* stem diameter when grown in wet vs dry (above water level) conditions. Graph by Yenhung Li, with permission.

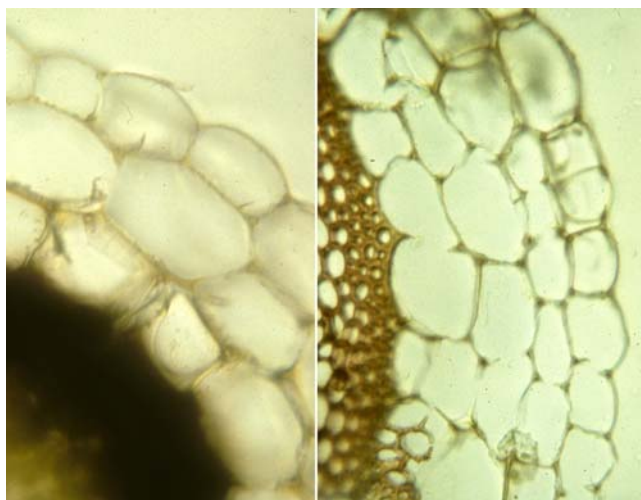


Figure 30. *Sphagnum magellanicum* stem cross sections showing outer hyaline layers. Left: stem grown in water; right: stem grown above water. Photos by Yenhung Li, with permission.



Figure 31. *Sphagnum papillosum*, a drought-resistant species that develops additional rows of cells when above water. Photo by David T. Holyoak, with permission.



Figure 32. *Sphagnum magellanicum*, a drought-tolerant species that develops additional rows of cells when above water. Photo by Michael Lüth, with permission.

Paraphyllia

Paraphyllia (Figure 33) are small green outgrowths on stems of some pleurocarpous mosses. They are useful taxonomic characters, permitting us to separate the sometimes lookalikes of *Pleurozium schreberi* (lacking paraphyllia; Figure 34) from *Hylocomium splendens* (having paraphyllia; Figure 35-Figure 36). But what is their function? The most logical is that of increasing water transport and reducing evaporation. There have been no tests to determine the value of their photosynthetic ability. And how often do they function as propagules, easily broken from the stems when dry? Do they form new plants under those conditions?

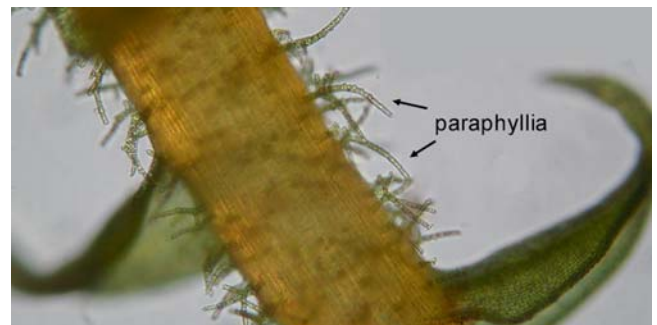


Figure 33. Stem of *Thuidium* sp. showing paraphyllia. Photo by Paul Davison, with permission.



Figure 34. *Pleurozium schreberi*, a moss that lacks paraphyllia. Photo by Janice Glime.



Figure 35. *Hylocomium splendens*. If you look carefully at the lowest visible part of the red stem in the center, you can see small bits of green paraphyllia. Photo by Rosalina Gabriel, with permission.

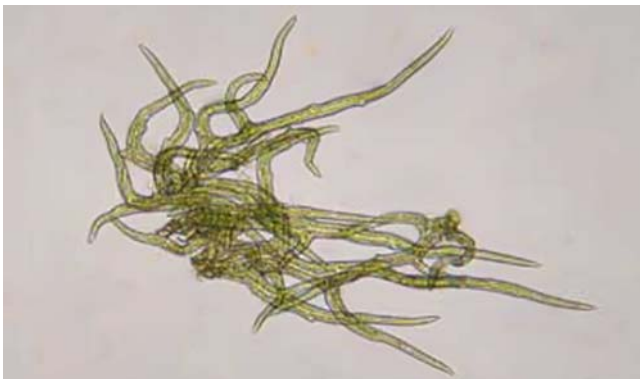


Figure 36. *Hylocomium splendens* paraphyllia. Photo from Botany Department website, University of British Columbia, BC, Canada, with permission.

Leaf Margins

Margins of leaves can be flat, **involute** (rolled upward; Figure 37), **revolute** (rolled under; Figure 38-Figure 39), and **bordered** or **unbordered**. The borders can be one cell thick or multiple cells thick. The whole leaf can be **inrolled** (rolled upward; Figure 40-Figure 41), folded (see Keels below), or flattened. And the borders can have teeth or be smooth. Some functions for these will be discussed in the chapter on Water Relations (Chapter 7-4, Vol. 1), but this chapter would not be complete without some consideration of them.

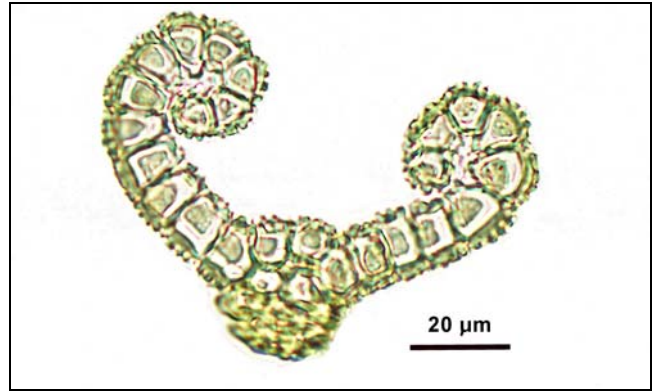


Figure 37. *Weissia controversa* leaf cross section showing involute margins. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.



Figure 38. *Bryoerythrophyllum recurvirostre* leaf cross section showing revolute leaf margins. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.



Figure 39. *Ceratodon purpureus* showing revolute leaf margins. Photo by Malcolm Storey, through Creative Commons.



Figure 40. *Dicranum muehlenbeckii* showing the curled, inrolled leaves. Photo by Michael Lüth, with permission.



Figure 41. *Dicranum muehlenbeckii* leaf cross section showing inrolled leaf. Photo by Michael Lüth, with permission.

Borders or Not

Bryophytes distinguish their leaf borders in a number of ways. While many lack special border cells (Figure 42), they may still have teeth on the border, as discussed below. Others may lack specialized cells but have margins that are more than one cell thick (Figure 49). And those with borders typically have elongate cells (Figure 43-Figure 44) that differ from lamina cells. These specialized border cells may have teeth or lack them.

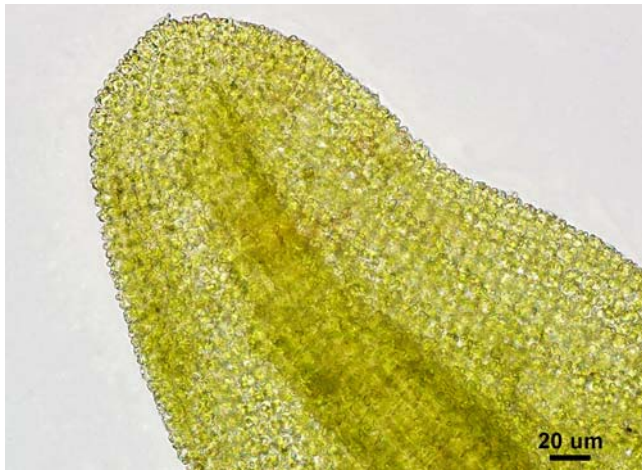


Figure 42. *Barbula convoluta* leaf with no border and with papillose cells and a costa. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.



Figure 43. *Mnium spinosum* leaf showing border with colored elongate cells contrasting with nearly isodiametric leaf lamina cells. Photo by Michael Lüth, with permission.

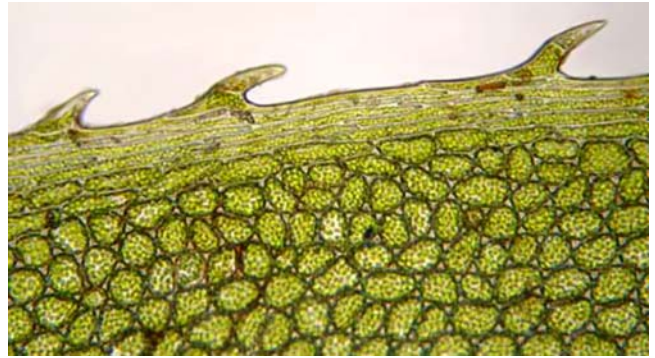


Figure 44. *Plagiomnium insignis* showing border that is several cells wide with elongate cells that contrast with the isodiametric lamina cells. Photo from Botany website, University of British Columbia, BC, Canada, with permission.

Special border cells are rare among tracheophytes, so this suggests that their presence may indicate a function in bryophytes that is not useful in tracheophytes. In fact, it is likely that this is true. Kürschner (2004) described the contortions and shrinkage of the leaf lamina in **Pottiaceae** (Figure 45-Figure 46) and **Grimmiaceae** (Figure 47-Figure 49). These contortions are typically dependent on the leaf border. As the lamina shrinks while drying, the border remains firm and does not shrink. Hence, the shrinking lamina cells pull and tug on the borders and a twisted leaf results. These leaves wind around the stem helically, benefitting from protection by the stem and reducing further desiccation and protecting against solar radiation. In desert habitats, the adhering sand grains are removed as the twisting leaves respond to water uptake and straighten during a rainfall (Scott 1982).



Figure 45. *Tortula intermedia* (Pottiaceae) hydrated. Photo by Michael Lüth, with permission.



Figure 46. *Tortula intermedia* (Pottiaceae) dry with leaves twisted around the stem. Photo by Michael Lüth, with permission.

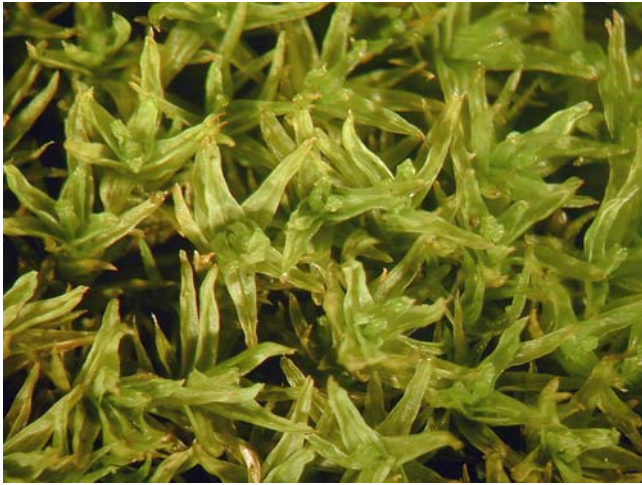


Figure 47. *Grimmia anomala* (Grimmiaceae) showing hydrated leaves that spread widely around the stem. Photo by Michael Lüth, with permission.



Figure 48. Dry *Grimmia anomala* (Grimmiaceae) showing leaves twisted around the stem. Photo by Jan-Peter Frahm, with permission.

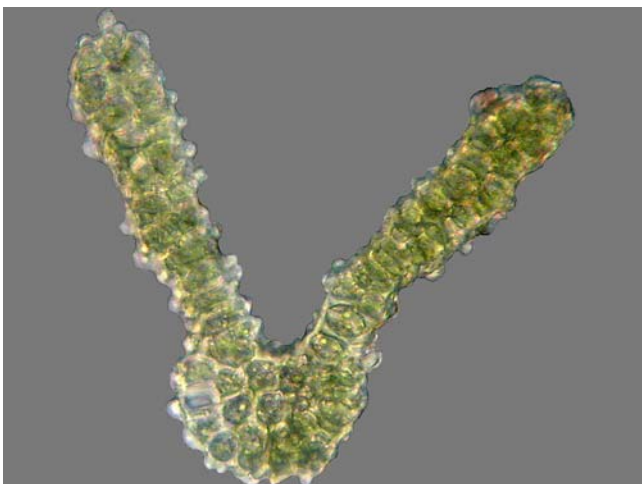


Figure 49. *Grimmia anomala* (Grimmiaceae) leaf cross section showing areas that are more than one cell thick, especially at the margin. The thickenings may contribute to the way it twists around the stem when dry. Note that the margin consists of a double layer of cells, giving the margin rigidity. Photo by Michael Lüth, with permission.

Marginal Teeth

Marginal teeth in tracheophytes seem to have multiple functions. In tracheophytes, marginal teeth are responsive to temperature (Royer & Wilf 2006; Royer *et al.* 2012). Using 3549 tracheophyte species from six continents, they determined toothed species are more likely to be deciduous, thin leafed, of low leaf mass per area, with ring-porous wood, and have a high leaf nitrogen content. Trees in the canopy are most likely to be sensitive to temperature as a determinant of leaf-margin state compared to shrubs and herbs. Hence, leaf thinness and deciduousness as well as temperature are linked to having teeth. Royer *et al.* argue that by being thin and having thin tissues in teeth along the margins, these deciduous leaves can return their contents to the ecosystem quickly. Perhaps the thin margins permit fungal and bacterial colonies to get established quickly?

Yet another hypothesis was tested by Baker-Brosh and Peet (1997). They observed that teeth were rare in tropical moist forests but frequent in temperate deciduous forests. They hypothesized that in those forests where leaves had to grow anew each year the teeth and lobes served as the site of early season photosynthesis in new leaves. Using $^{14}\text{CO}_2$ and autoradiography, they determined that eight species with prominent teeth or lobes did indeed exhibit early season photosynthesis on the margins, whereas in those with entire margins (no teeth; 4 species) there was no early season photosynthesis on the margins. However, seven species that were toothed or lobed likewise lacked early season photosynthesis on the margins. Royer and Wilf (2006) demonstrated that teeth were advantageous for early season photosynthesis in temperate climates. Could there be similar early season photosynthetic behavior to aid growth of new leaves in some mosses, particularly if margins at that stage are predominantly green (Figure 50-Figure 52)?

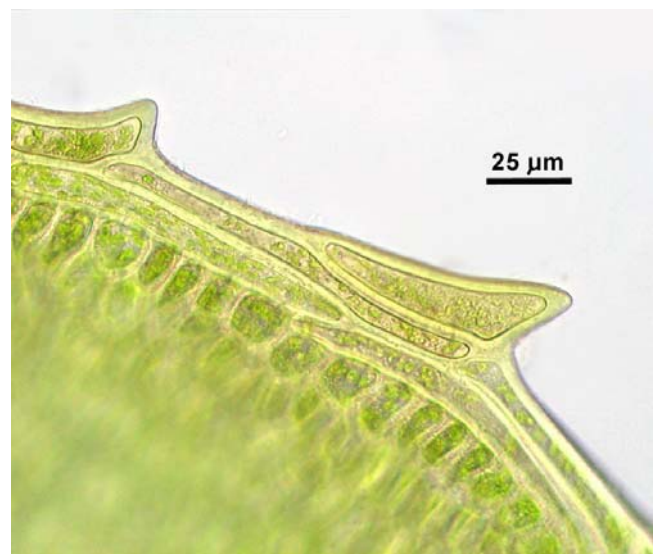


Figure 50. *Plagiomnium undulatum* leaf border showing photosynthetic marginal teeth. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.



Figure 51. *Plagiommium undulatum* showing small leaves at apex where teeth may help in photosynthesis in early development. Photo from <www.aphotofauna.com>, with permission.

Royer *et al.* (2009) further explored the role of teeth in the Australian subtropical rainforest trees. Using 227 sites, they found a correlation between humidity and number of toothed species, with the greatest occurrence of toothed species in the riparian zone and the fewest at the drier ridge tops. They attribute the relationship to the availability of water. Could it be that toothed species of these large leaves lose water more easily due to the increased surface area, negating the early spring advantage in dry sites? Would this incur the same problem in bryophytes, or might the teeth actually confer a water advantage – a site for collecting and absorbing water much like the hair tips discussed below? I am aware of no quantitative study to test this hypothesis in bryophytes.

Applying these tracheophyte principles to bryophytes could bring interesting insights, but I am unaware of any attempt to test the correlations.

In bryophytes, teeth can occur along the margins [singly (Figure 50) or doubly (Figure 52)], but also occasionally projecting from the leaf lamina (Figure 53-Figure 55) or costa (Figure 55-Figure 56).



Figure 52. *Mnium spinosum* leaf showing double teeth on leaf margin. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

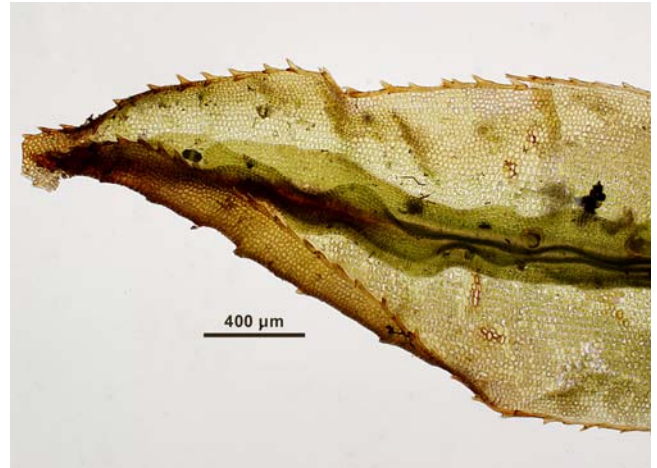


Figure 53. *Atrichum selwynii* leaf showing teeth projecting from the dorsal side of the leaf lamina. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.



Figure 54. *Atrichum undulatum* leaf showing teeth in diagonal rows on dorsal side. Photo by Jutta Kapfer, with permission.



Figure 55. *Atrichum undulatum* leaf showing teeth (arrow) on dorsal side. Note also the teeth on the costa. Photo by Jutta Kapfer, with permission.



Figure 56. *Mnium spinosum* back of costa showing tooth on costa. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

Among tracheophytes, leaf teeth are postulated to mimic effects of herbivory and thus to discourage additional herbivores on a leaf that has already been eaten. This proposed deterrent may have credence in the fact that antiherbivore compounds often are inducible (Karban & Baldwin 1997; Karban *et al.* 1997; Ceh *et al.* 2005), so a herbivore might recognize that the leaf (or alga) has been eaten and will taste bad without the herbivore having to take a sample. The argument is that the teeth give the appearance that the leaf has been nibbled before.

Could this tracheophyte herbivore deterrent of teeth have a role in bryophytes? Might herbivores consider it a signal that the leaves will taste bad? We don't even know if antiherbivore compounds in bryophytes are inducible. But then, perhaps the insects don't know either and assume the bryophytes behave like tracheophytes. And do these bryophyte teeth really look like evidence of herbivore browsing? Or do they possibly have the deterrent effects that hairs and spines have on browsing by large herbivores? Might they deter such soft-bodied herbivores as snails? It would be easy to see if snails choose to crawl over bryophyte leaves without such teeth in preference to those with them. *Atrichum undulatum* would be a good test subject with its teeth on the lamina (Figure 53-Figure 55).

Liverworts

And what about the lobes and teeth of **leafy liverworts** (Figure 57)? Do they have any adaptive value? Could they also have antiherbivore functions? Do they serve to hold water on the leaf surface? Or are they just useful tools for bryophyte taxonomists?

In the leafy liverwort genus *Plagiochila*, habitats in North America differ from those in the tropics and so do the teeth. In North America, *P. porelloides* (Figure 58-Figure 59) lives next to or in water and has small or almost no teeth. In the tropics, where there are many species in the genus, this genus lives on tree trunks and sides of boulders where conditions may be almost xeric. Most of these species have large teeth (Figure 60). When it rains, these liverworts can become quite saturated. Do the teeth help the leaves to hold droplets of water? Could their added surface area provide evaporative cooling? Or is this again an early season adaptation to enhance photosynthesis?

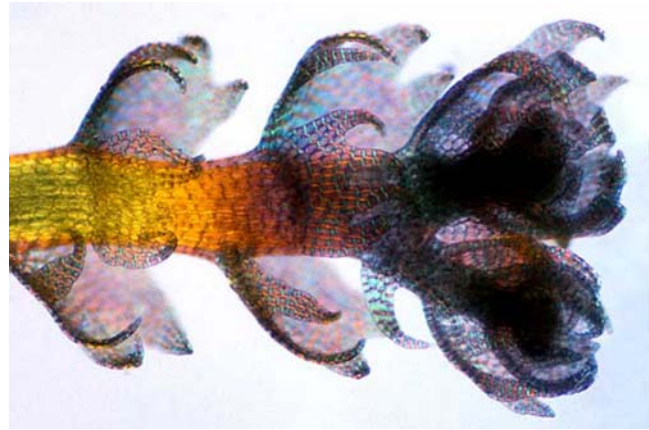


Figure 57. Leafy liverwort showing lobes that curl toward the stem. One can easily imagine these leaves trapping a cohesive drop of water, then slowly bending inward as that water droplet shrinks. Photo by Bill Malcolm, through Creative Commons.



Figure 58. *Plagiochila porelloides*, a species that grows in moist areas like stream banks in the Northern Hemisphere. Note that the teeth are much smaller than in most tropical species. Could teeth provide evaporative cooling? Photo by Dick Haaksma, with permission.

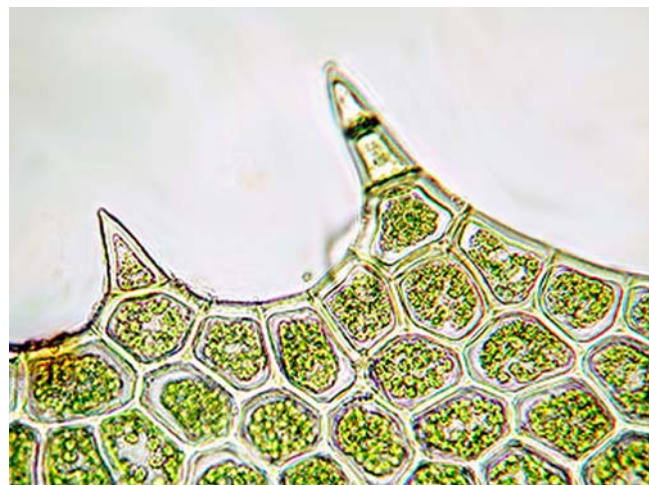


Figure 59. *Plagiochila porelloides* leaf teeth showing the smaller size in this streamside and wet habitat species compared to tropical epiphytes and epiliths. Photo from Botany Department website, University of British Columbia, BC, Canada, with permission.



Figure 60. *Plagiochila raddiana* from the Neotropics. How do these teeth function for the tropical epiphytic and epilithic species? Photo by Michael Lüth, with permission.

Some species of liverworts have deep lobes. In some cases these are curved toward the stem (Figure 61) and one can imagine that they help to hold drops of water, clinging to them and curving further inward as the drop decreases in size (Figure 62). Such structure could provide a water reservoir for the leaf, permitting photosynthesis for a longer period of time. If the convex surface faces the light, the water reservoir could permit photosynthesis to continue for a longer period of time without interfering with light capture, while permitting CO₂ to enter from the surface opposing the water drop.



Figure 61. *Lepidozia reptans*, a relative small species with leaves in a size range where they could trap a cohesive water drop. Teeth may aid in holding that water next to the leaf. Photo by Walter Obermayer, with permission.



Figure 62. Wet *Ptilidium ciliare* showing teeth clinging to the leaf beneath, presumably aiding in water retention. Photo by Des Callaghan, with permission.

Presumably, size affects the utility of teeth and lobes. If one compares the large size of the leaf and its lobes in *Lophocolea* (Figure 63) with those in *Cephalozia* (Figure 64), it appears their functionality should work differently. Small droplets of water are harder to break up than large ones. Does this have any bearing on utility, size, and location of the lobes? Would long, thin lobes on large leaves direct water off the leaf, permitting CO₂ to enter the cells, behaving like the drip tips of some tropical leaves?

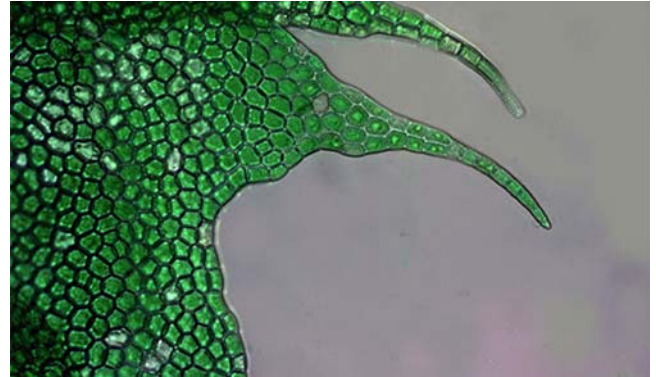


Figure 63. *Lophocolea bidentata*, a relatively large species showing leaf lobes. Might these aid in holding drops of water? Photo by Aimon Niklasson, with permission.

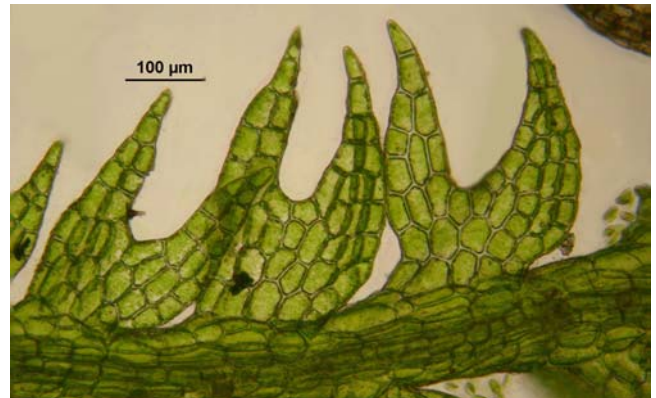


Figure 64. *Cephalozia bicuspidata*, a much smaller species than *Lophocolea bidentata*, showing leaf with deep lobes. Could these lobes provide a means of holding onto a drop of water, much as a diving beetle holds onto a bubble of air? Photo by Hermann Schachner through Wikimedia Commons, with permission.

Let's return to the consideration of moisture relationships and number of species with teeth. This might be simplest to demonstrate with epiphytes. In the temperate zone, where epiphytic positions can impose long drought periods, most of the large leafy liverworts have entire leaf margins, e.g. *Frullania* (Figure 65), *Porella* (Figure 66), and *Radula* (Figure 67). In the tropics, *Plagiochila* (Figure 68) is very common, with many species, and most of these have rather large teeth. Tropical rain forests have long seasons of rainy weather that can maintain the moisture among these liverworts, followed by a long season of drought when the liverworts can remain dormant. Temperate species, on the other hand have the risk of drying before they have repaired the damage from the last drought. Which strategy – teeth or no teeth – permits them to hold water longer? What fun for experimentation!

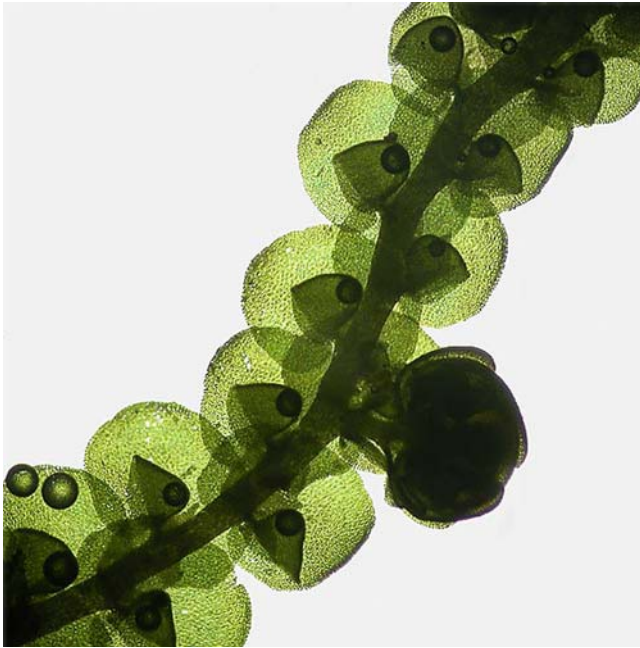


Figure 65. *Frullania dilatata* showing lobules and entire margins (no teeth or lobes). Photo by Walter Obermayer, with permission.



Figure 66. *Porella cordaeana* showing entire leaf margin. Photo by Jan-Peter Frahm, with permission.



Figure 67. *Radula* from the Neotropics showing entire leaf margins. Photo by Michael Lüth, with permission.



Figure 68. *Plagiochila adiantoides* from the Neotropics showing toothed leaf margins. Photo by Michael Lüth, with permission.

One might argue that in liverworts like *Nowellia curvifolia* (Figure 69), the long lobes provide a stalk for the clusters of gemmae produced at their tips. Such positioning for the gemmae might make it easier for them to escape the plant and travel a greater distance.



Figure 69. *Nowellia curvifolia* showing gemmae positioned at the ends of narrow leaf lobes. Photo by Paul G. Davison, with permission.

Hair Tips

Many bryophytes in dry habitats have hair tips on the leaves (Figure 70-Figure 71). One suggestion for their role is that they are able to reflect sunlight (Kürschner 2004). This can protect the underlying cells from sun damage when they are dry and the leaves are compressed against the stem. And in many species, when the plants are dry the leaves twist around the stems so that each hair overlaps the leaf above it (Figure 72).

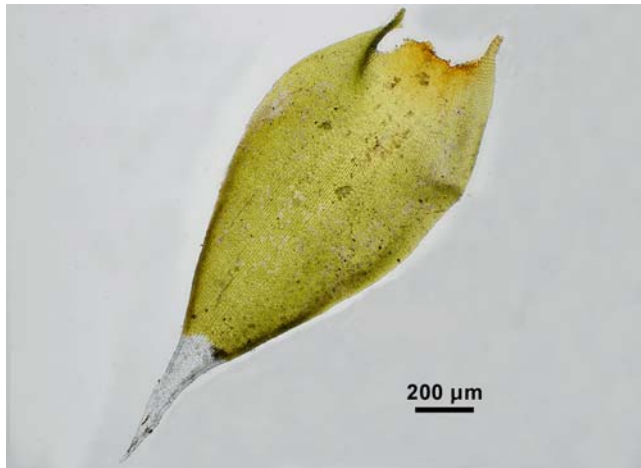


Figure 70. *Hedwigia ciliata* leaf showing translucent hair point. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.



Figure 71. *Hedwigia ciliata* with wet plants on the upper left and dry ones on the edge of the colony (lower right). Note how the dry leaves cling to the stem compared to the spreading wet leaves. Photo by Janice Glime.



Figure 72. *Grimmia decipiens* showing array of hairs that help fill in spaces between stems. Photo by Des Callaghan, with permission.

A second function has been suggested – that the hair points may help to absorb condensed water vapor from fog and dew (Figure 73-Figure 75) (Kürschner 2004). This phenomenon is well known from physics – small droplets accumulate around thin wires – and on fine hairs. To this role, I would add that the hairs may provide additional capillary spaces that gain water in rain as well and hold it there for longer periods of time, preventing evaporation from the leaves.



Figure 73. *Grimmia cf. pulvinata*, lightly covered with dew, on churchyard wall. This picture supports the notion that the hairs can act to collect dew that can eventually drip down into the moss mat. In areas with low precipitation and frequent fog, this can be the only source of water for some mosses. Photo by Brian Eversham, with permission.



Figure 74. *Grimmia horrida* habitat at edge of fog in northern Portugal. Photo by Michael Lüth, with permission.



Figure 75. *Campylopus introflexus* collecting water drops on the fine hairs. Photo by Michael Lüth, with permission.



Figure 76. *Tortula muralis* with hair tips trapping water droplets. Photo by Christophe Quintin, through Creative Commons.

If we examine the picture of *Grimmia* from Scotland (Figure 77), we can see a third possible function. Note that the frost is held away from the leaves. Frost and ice crystals are very hygroscopic and can draw water out of the leaves as they do from the foods in your freezer. The hairs seem to function, at least in this case, to keep the frost from contacting the leaves, thus avoiding their potential desiccating effect. The same is often seen in leaves of early spring perennial flowers.



Figure 77. *Grimmia* capsules and frost at Dunkeld, Scotland. Photo by Allan Water.

As I sorted through images, I was struck by another potential purpose for some hairs. As you will learn in Chapter 7, bryophytes survive desiccation much better than their tracheophyte counterparts. But when they are rehydrated, they must repair damaged membranes, and this seems to take about 24 hours. A short misting or very light rain that evaporates right away may not provide enough hours for repair before the bryophyte is once again desiccated, hence wasting the energy expended in its failed attempt. Hairs can fill in spaces between apices (Figure 78), trapping water droplets and keeping them from entering the moss mat, thus preventing a hydrated period that is too short, or perhaps keeping the water at the tip to be absorbed slowly over time (Figure 79).



Figure 78. *Grimmia* at Goudini Spa, South Africa. With hairs in this position, they can capture the cohesive water drops (Figure 79) and prevent them from entering the moss mat during a light shower. When the storm lasts longer, the weight and size of the droplets will finally force them through the hairs. Photo by Janice Glime.



Figure 79. *Pohlia wahlenbergii* with cohesive water drops. Note that these drops are mostly too large to penetrate the mat and hence remain at the surface, held together by their own cohesive forces. Photo by J. C. Schou, through Creative Commons.

Finally, I suggest that hair points, at least in some species, can deter some kinds of herbivores. We know that invertebrate herbivores are deterred by hairy leaves of tracheophytes (Karban & Agrawal (2002) and that spiny leaves deter ungulates (Obeso 1997). It is not unreasonable to assume that they can confer similar advantage to bryophytes, particularly when hair points overlap extensively as in *Grimmia arenaria* (Figure 80).



Figure 80. *Grimmia arenaria*, demonstrating long hairs that might protect from bright sun or prevent desiccation. Photo by Des Callaghan, with permission.

Costae

The **costae** are the moss versions of midribs (Figure 81). They are absent in liverworts. Their functions may include movement of water from base to tip of the leaf, or perhaps from tip to base. This can be surmised by the elongate structure of the cells (Figure 82) compared to the shortness of leaf lamina cells in many species. I have referred to base to tip transport because it is the base where water can accumulate in the leaf axil and receive water from the stem through its external movement of water. But in some plants, water might move into the leaf at the tip, possibly absorbed through the apical leaf hair, but empirical data to demonstrate this seems to be lacking.

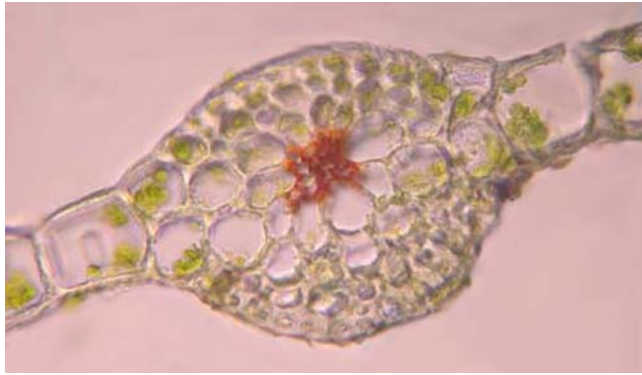


Figure 81. *Rhizomnium glabrescens* leaf cross section showing costa. Photo from Botany Department website, University of British Columbia, BC, Canada, with permission.

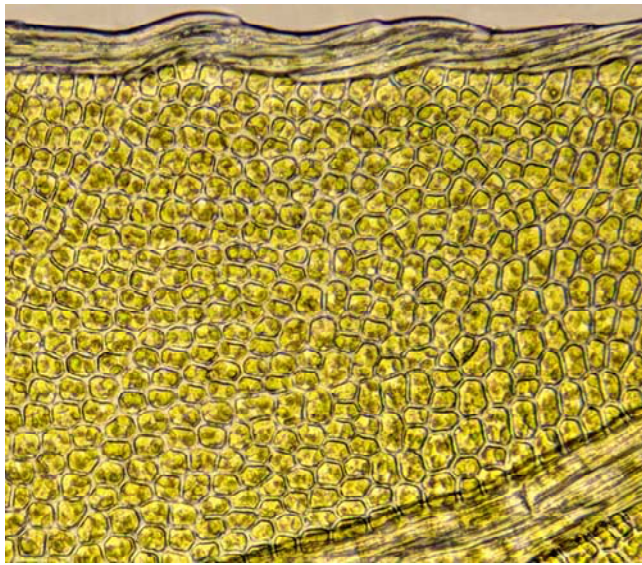


Figure 82. *Fissidens bryoides* leaf cells showing elongate cells of costa in lower right. Photo by Dick Haaksma, with permission.

I have constantly been struck by the attempts of ecologists to find a single explanation or advantage for a particular strategy for plants or animals. I am convinced that many of these strategies/structures persist because they provide small advantages for multiple functions. And certainly some are advantageous in some situations or years, but not in others. They may at times even be disadvantageous.

Proctor (2010) points out that in **Sematophyllaceae**, some members have a costa and others do not. The same is true in the **Fontinalaceae**. In the latter family, the costa separates the costate genera *Dichelyma* (Figure 83) and *Brachelyma* (Figure 84), both occurring in inundated areas but living mostly above water, from the ecostate genus *Fontinalis* (Figure 85), a genus that spends most of the year under water. Olsson *et al.* (2009) have shown that in the **Neckeraceae** reduction of the costa has recurred in all three main clades. Proctor (1979) concludes that the presence or absence of a costa, as well as the shape of leaf cells, must have functional consequences, but we are uncertain how important these are for mechanical support vs conduction within the leaf, not to mention simply chance occurrence relating more to ancestry than to (current) function.



Figure 83. *Dichelyma falcata*, a member of the **Fontinalaceae** with a costa. Photo by Michael Lüth, with permission.



Figure 84. *Brachelyma subulatum*, a member of the **Fontinalaceae** with a costa and keeled leaves. Photo by Janice Glime.



Figure 85. *Fontinalis hypnoides* showing absence of costa. Photo by John Game, with permission.

I was surprised to find that when grown in my artificial stream with considerable air exposure, *Fontinalis* produced short costae. Bruce Allen once told me he had also sometimes found *Fontinalis* leaves from nature that had short costae. To me this suggests that something suppresses the development of the costa and that under certain conditions that suppression doesn't function. That would imply that the costa came first and that a suppressor developed later. That suppressor is most likely water, which not only affects hydration, but also affects CO₂ uptake, oxygen concentration, and escape of gases such as the developmental hormone **ethylene**.

Costae can provide strength for a leaf. It can represent a tough tissue not eaten by herbivores. It is the structure that remains on leaves of aquatic species such as those of *Hygroamblystegium* (Figure 86-Figure 87) when exposed to rapid flow and suspended solids. But is any of these adaptive in any way? Possibly. If the costa is capable of growth into a new plant, it could become a dispersal agent. It could also provide photosynthetic tissue when leaf lamina tissue has been eaten or eroded. But there is no empirical proof that these things occur or if so, are they of any consequence.

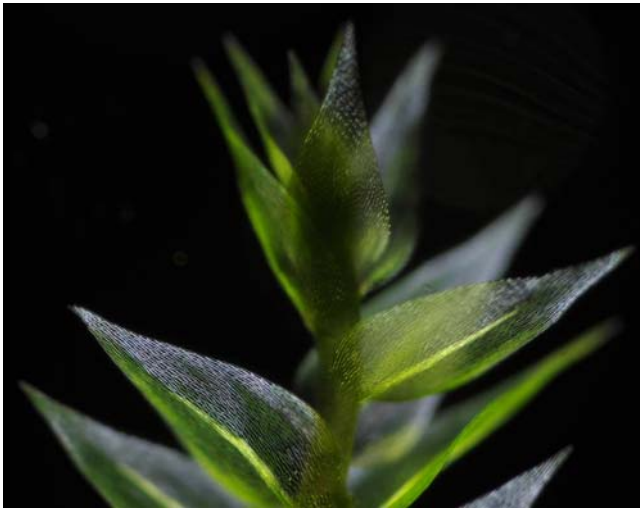


Figure 86. *Hygroamblystegium tenax* showing thick costa in leaves. Photo by Martha Cook, with permission.



Figure 87. *Hygroamblystegium fluviatile* showing dark costae left from eroded leaves. Photo by Michael Lüth, with permission.

Some amphibious bryophytes actually have reduced or lost costae when they have grown in the water. For example, Rod Seppelt (Bryonet 24 June 2012; Seppelt &

Selkirk 1984) observed that the costae of *Bryum pseudotriquetrum* (Figure 88-Figure 89) were shorter and weaker on aquatic specimens from lakes in Antarctica compared to those growing out of water. He also reported inducing absence of costae and change in leaf shape in *Bryum argenteum* (Figure 90) in culture, with temperature playing a major role in inducing leaf changes; lower temperatures resulted in wider leaves. Furthermore, at 4°C the costa was absent. Clearly in some species the environment can affect how the costa develops. But what does it mean for the plant?



Figure 88. *Bryum pseudotriquetrum* showing strong costa of the terrestrial form. Photo by Des Callaghan, with permission.



Figure 89. *Bryum pseudotriquetrum* leaf showing costa that becomes shorter and weaker in Antarctic lakes. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

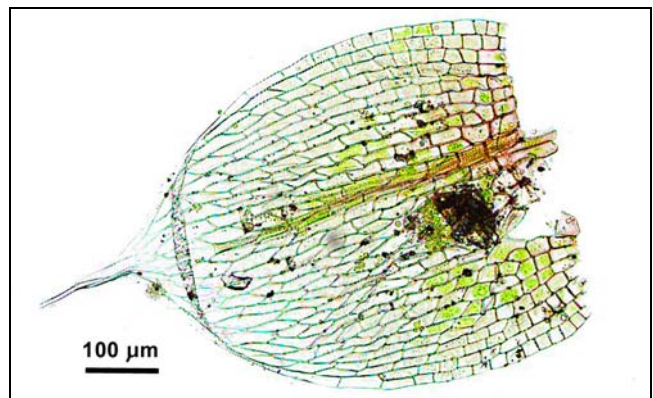


Figure 90. *Bryum argenteum* leaf showing well developed costa of a terrestrial form. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

In the genus *Dicranum* (Figure 91-Figure 96), the costa varies widely, with almost no differentiation in *Dicranum rhabdocarpum* (Figure 91) to phalanges along the costa in *Dicranum scoparium* (Figure 96). In other members of the *Dicranaceae*, for example *Pilopogon peruvianus*, the costa can occupy most of the leaf width (Figure 97).



Figure 91. *Dicranum rhabdocarpum* leaf cross section showing absence of papillae. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.



Figure 92. *Dicranum muehlenbeckii* leaf cross section showing relatively smooth cell surface. Photo by Michael Lüth, with permission.



Figure 93. *Dicranum brevifolium* leaf cross section showing costa and mammillate cells. Photo by Michael Lüth, with permission.



Figure 94. *Dicranum dispersum* leaf cross section showing costa and thickened margins. Photo by Michael Lüth, with permission.



Figure 95. *Dicranum fuscescens* leaf cross sections showing costa and papillose leaf cells. Photo by Michael Lüth, with permission.

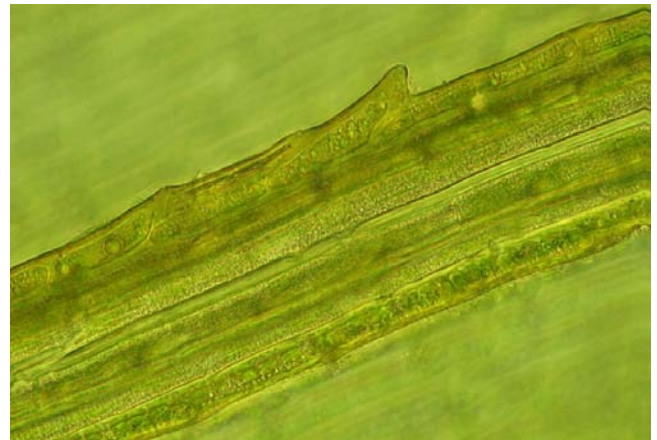


Figure 96. *Dicranum scoparium* teeth on back of leaf costa. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.



Figure 97. *Pilopogon peruvianus* showing a costa that occupies most of the leaf. Photo by Michael Lüth, with permission.

Glenn Shelton (Bryonet 15 June 2012) contended that mosses tend to evolve from having multiple costae (Figure 98) to few (single or none). He and colleagues have found a number of tricostate mosses from the Early Cretaceous of Vancouver Island, B.C., Canada, some apparently pleurocarpous, as evidenced by a high degree of branching (including pinnate) and cell morphology. On the other hand, it appears that costa number is quite plastic among major moss lineages – and even within species (see above). And Ben Tan (Bryonet 30 June 2012) enters a word of caution – that folds or plicae at the leaf base can look like short costae, so one must be careful in interpreting fossil costae.

Shelton (Bryonet 15 June 2012) explains that one theory is based on the premise that the costa gives rigidity to the leaf and that multiple costae provide more rigidity. This assumes, then, that the need for this rigidity has been lost in some species. The theory also considers evolution from complex leaf structure to a simpler structure – **reduction**.



Figure 98. *Vesicularia montagnei* showing short, double costa. Photo by Tan Sze Wei, Aquamoss website <www.aquamoss.net>, with permission.

Perhaps Kürschner (2004) has the right idea for some species. He notes that the costa is often shiny (Figure 99- Figure 100) in mosses growing in xeric sites. Hence, he suggests that the costa may reflect the solar radiation and thus reduce both evaporation and heat stress. I would need

proof to see how a narrow costa could have much impact, and it seems that xeric costae are often darker than the leaf (Figure 99- Figure 100), suggesting they might absorb more heat than the lamina.



Figure 99. *Syntrichia andicola* showing shiny costa. Photo by Michael Lüth, with permission.



Figure 100. *Syntrichia andicola* showing costa of leaf. Photo by Michael Lüth, with permission.

Zander (Bryonet 25 June 2012) reminded us of the perspective of Gould (2002) that there are minimum constraints on size – a developmental wall to small size for particular organisms. He considers that the elimination of superfluous costal material might depend on size. As leaves get smaller, the costa necessarily gets smaller, and it might no longer serve the same function or advantage it did in larger leaves. Zander points out that acrocarpous mosses usually have costae, but that pleurocarpous mosses may or may not. Is this a size difference, or a difference in phylogenetic history? And perhaps costae persist, or not, because some other linked trait is affected by some selection pressure that has changed over time.

Lamellae

Lamellae (Figure 101- Figure 113) can greatly increase the surface area of a leaf. They provide numerous surfaces, exposed on both sides for absorption of light and especially CO₂ and provide capillary spaces for taking up and holding water.

Members of the family **Polytrichaceae** are defined by the presence of lamellae (Figure 101-Figure 106), but other genera in scattered families have them as well. These include *Aloina* (Figure 107), *Crossidium* (Figure 108-Figure 109), *Pterygoneurum* (Figure 110-Figure 112), and some *Syntrichia* (Figure 113).



Figure 101. *Atrichum undulatum* leaf lamellae. Photo by Walter Obermayer, with permission.



Figure 102. *Atrichum undulatum* leaf cross section showing lamellae. Photo by Walter Obermayer, with permission.



Figure 103. *Polytrichastrum formosum* leaf cross section showing lamellae. Photo by Michael Lüth, with permission.

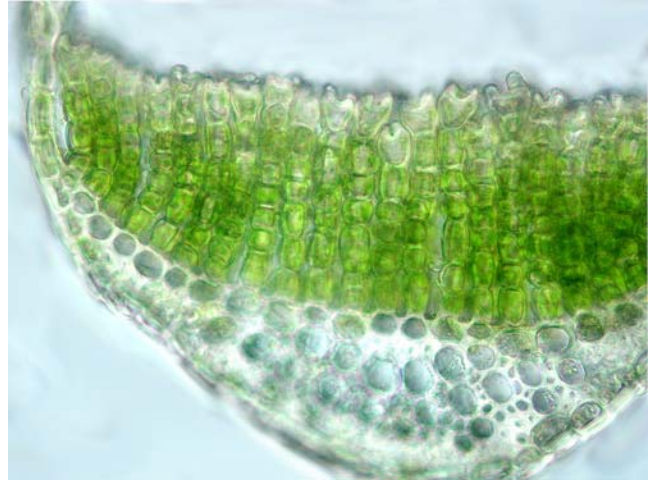


Figure 104. *Polytrichum commune* leaf cross section showing lamellae. Photo by Michael Lüth, with permission.



Figure 105. *Polytrichum hyperboreum* showing leaf lamina rolled over the lamellae. Photo by Michael Lüth, with permission.

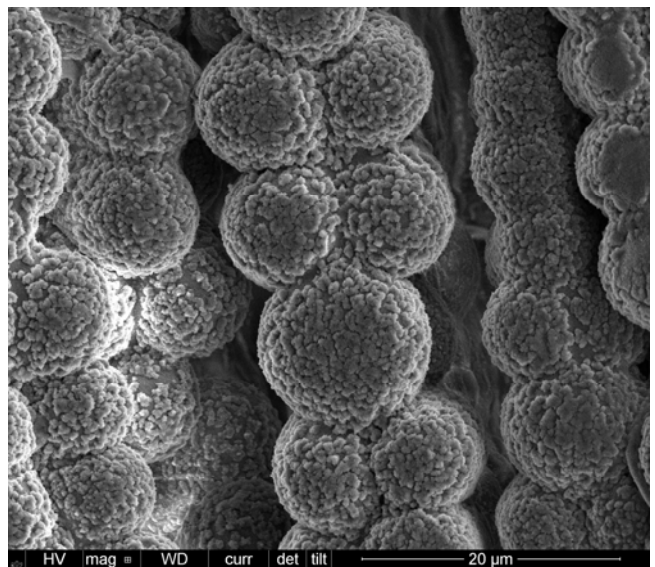


Figure 106. *Dendroligotrichum squamosum* SEM showing tops of lamellae. Photo courtesy of Jeff Duckett and Silvia Pressel.



Figure 107. *Aloiina rigida* with lamellae within the inrolled leaf margins. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.



Figure 108. *Crossidium squamiferum* showing leaves that appear to be succulent due to lamellae. Note how the leaf curves inward in this species. Photo by Jan-Peter Frahm, with permission.



Figure 109. *Crossidium aberrans* leaf showing lamellae along costa. Photo by Michael Lüth, with permission.



Figure 110. *Pterygoneurum ovatum* showing fleshy, inrolled leaves that partially cover the lamellae. Photo by Kristian Peters, with permission.

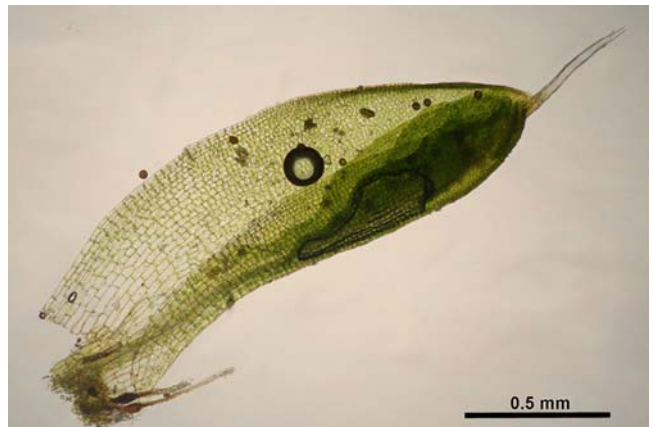


Figure 111. *Pterygoneurum ovatum* leaf showing lamellae in upper half. Photo by Hermann Schachner, through Creative Commons.

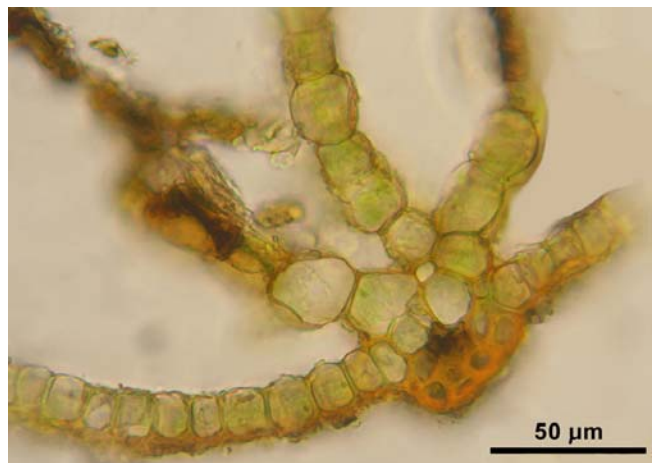


Figure 112. *Pterygoneurum ovatum* leaf cross section showing leaf lamellae. Photo by Hermann Schachner, through Creative Commons.



Figure 113. *Syntrichia papillosa* leaf showing tips of lamellae. Photo by Des Callaghan, with permission.

Kürschner (2004) suggests that the lamellae facilitate water conduction as well as storing water. These roles are in addition to their photosynthetic role. Proctor (2005) demonstrated that the lamellae in **Polytrichaceae** (Figure 101-Figure 106) are important for the absorption of CO₂, increasing typical uptake by six times that of the projected leaf area, whereas in unistratose leaves of most other bryophytes, CO₂ uptake is limiting. This permits the **Polytrichaceae** to take advantage of high light intensity in open areas. Furthermore, these lamellate species experienced high non-saturation light levels, permitting them to take advantage of high intensity light. In a number of these species, including some of *Polytrichum* (Figure 105), the leaf margins fold over the lamellae, affording protection from excess UV light and preserving moisture. and space for CO₂ exchange.

Keels

Most leaves are slightly concave, some are flat, and some are folded over, forming a **keel** (Figure 114). The most striking of these is the keel in several species of the aquatic moss *Fontinalis*. The keel appears to give rigidity to the leaf, but when this species occurs in flowing water the keel often is abraded, leaving the leaf in nearly two pieces.



Figure 114. *Fontinalis antipyretica* showing keeled leaves. Photo by Li Zhang, with permission.

A modification of the keel occurs in the **Fissidentaceae** (Figure 115). This unique structure forms a

pocket on the apical edge of the leaf into which the succeeding leaf can partially fit. The double area of each leaf adds rigidity and provides capillary space that presumably holds water for a longer time. When the leaves overlap into the pockets, they can help to make the entire plant more rigid.



Figure 115. *Fissidens curvatus* showing pockets with succeeding leaves fitting into them in some cases. Photo by Tom Thekathyl, with permission.

Leaf Plications

Some genera are characterized by leaf plications (). These are typically folded like a Japanese fan. But what is the value of these plications? In tracheophytes, they can add strength. Consider lifting something with a sheet of paper. Then consider lifting the same thing with that same paper after it is fan folded. But is that kind of strength needed by a bryophyte leaf? Does it give a thin leaf a better ability to hold a drop of water?



Figure 116. *Coscinodon cribrosus* leaf with plications. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.



Figure 117. *Coscinodon cribrus* leaf cross section showing plications. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.



Figure 118. *Cratoneuron decipiens* leaf with plications. Photo by Michael Lüth, with permission.

Leaf Cells

Cell shape varies considerably, from small isodiametric cells (Figure 82) to large, nearly hexagonal ones (Figure 119) to elongate ones (Figure 120). Some cells have wall invaginations or wavy walls (Figure 121). Little mention has been made of the advantages of various cell types. One can imagine that elongate, narrow cells might move water more quickly with fewer walls to cross and formation of capillary space within the cell. I can't even imagine an advantage for the irregular wall shapes in *Racomitrium* (Figure 121). Bill Buck once asked me what I thought was the significance of the elongate cells in many pleurocarpous mosses. I couldn't give a good answer then, and now, several decades later, I still can't.

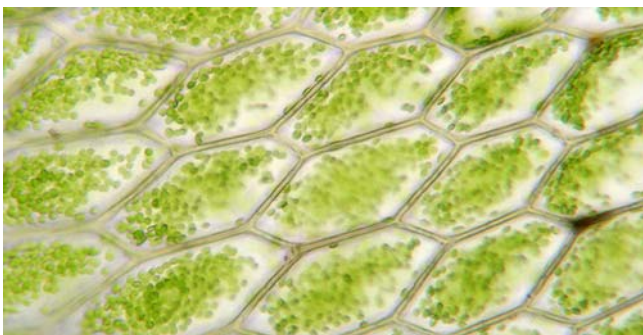


Figure 119. *Hookeria lucens* hexagonal leaf cells. Photo by Malcolm Storey <www.discoverlife.org>, through Creative Commons.



Figure 120. *Hygroamblystegium tenax* showing elongate cells. Photo by Martha Cook, with permission.

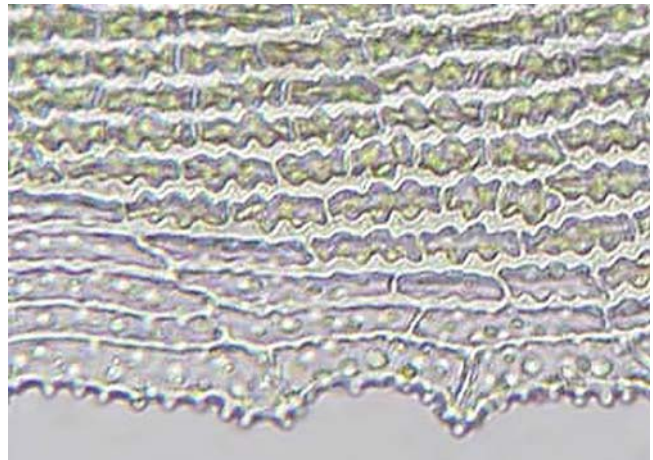


Figure 121. *Racomitrium canescens* cells showing wavy walls with invaginations. Photo from Botany Department website, University of British Columbia, BC, Canada, with permission.

Papillae

Many theories have been proposed for papillae, but little is available as experimental evidence to support them. The papillae have a number of shapes and forms (Figure 122-Figure 124), while varying in size and density. Based on this variability, it seems to me that their functions may not be the same in all species or under all conditions.

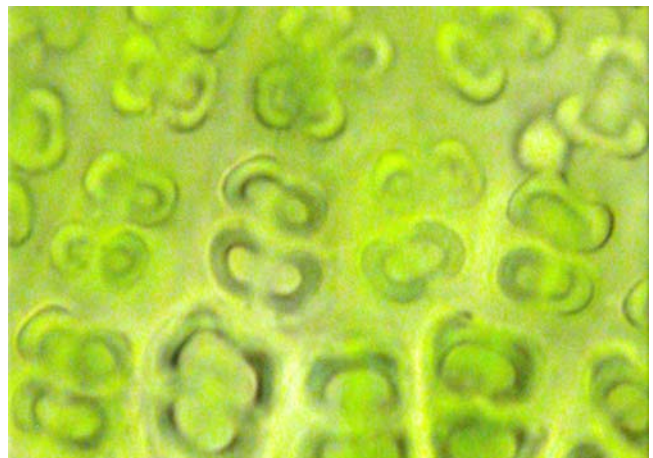


Figure 122. *Tortula muralis* leaf cells with C-shaped papillae. Photo by Walter Obermayer, with permission.

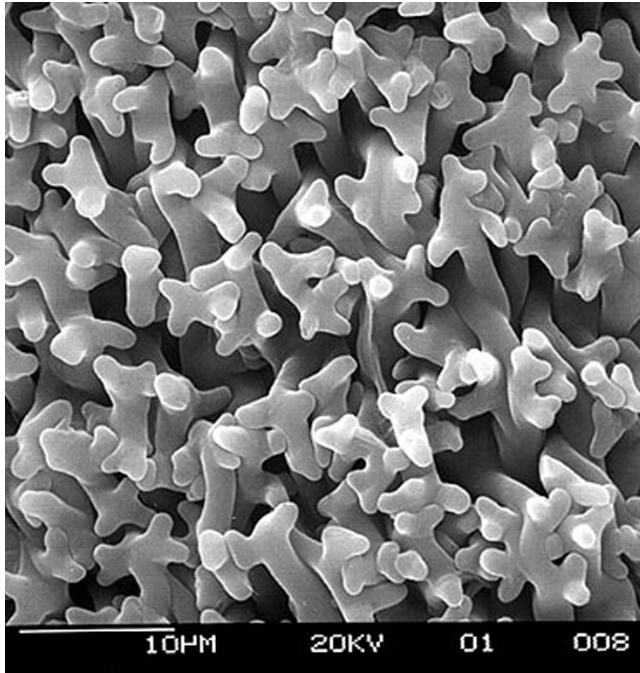


Figure 123. *Tortula muralis* SEM of branched papillae. It is easy to see how these papillae could scatter light and protect the chlorophyll during dry periods. Photo from Botany Department website, University of British Columbia, BC, Canada, with permission.



Figure 124. *Chrysoblastella chilensis* leaf cross section showing papillae and capillary spaces between them. Photo by Juan Larrain, with permission.

When lamina papillae are dense, they give the leaf a waxy, often succulent look (Figure 125). The dull surface most likely does the same to the sunlight as it does to our eyes – it bends the light rays, preventing them from making straight entry into the leaf cells and thereby reducing damage to the chlorophyll when the leaf is dry. When the leaf is wet, the capillary spaces fill with water and the leaf surface behaves more like a uniform translucent surface (Figure 126). At least that is how some of us have interpreted the behavior. In experiments in my lab with papillose leaves under the microscope, we found that wet leaves transmitted about twice as much light as dry leaves, supporting that hypothesis.



Figure 125. *Encalypta streptocarpa* illustrating the waxy appearance when dry caused by numerous papillae. Photo by Michael Lüth, with permission.

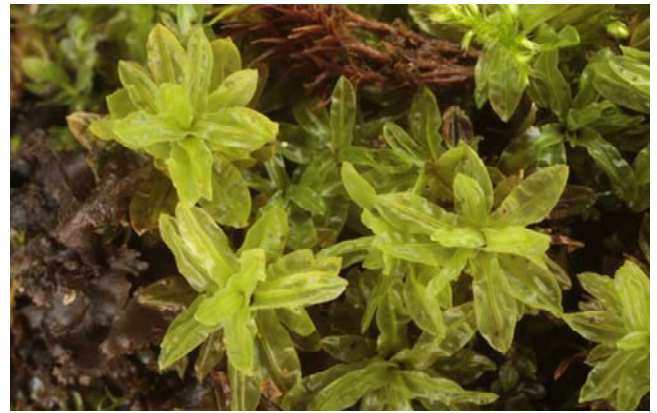


Figure 126. *Encalypta streptocarpa* showing translucent appearance of the leaf when wet. Photo by Jan-Peter Frahm, with permission.

In some, perhaps all, the papillae facilitate water uptake by providing capillary spaces (Proctor 1979; Longton 1988; Pressel *et al.* 2010; see Chapter 7-4), but they can also facilitate water loss (Pressel *et al.* 2010). The uptake is usually accomplished by the small channels between the papillae, but in *Andreaebryum macrosporum* (Figure 127), a small capillary channel goes through the papillae toward the cell and facilitates the rapid uptake of water during rehydration (Crandall-Stotler & Bozzola 1990, 1991).



Figure 127. *Andreaebryum macrosporum*, a moss for which papillae are known to aid in uptake of water. Photo from Botany website, University of British Columbia, Canada, with permission.

An Alternative to Papillae?

In the moss *Rhacocarpus purpurascens*, the leaf cell wall has an unusual structure. The wall has three layers that Pressel *et al.* (2010) interpret as "a supreme adaptation to exposed habitats." This moss lives where there are frequent alternations between drought and heavy precipitation. We know that *Sphagnum* experiences water logging that prevents photosynthesis, and Pressel *et al.* reasoned that this special wall structure in *R. purpurascens* prevents water logging. Its outer cell wall layer is porous, ensuring rapid water uptake and retention. The hydrophobic cuticle-like layer simultaneously prevents water logging. The middle layer serves to extend the period of cell hydration, permitting active metabolism under drying conditions. The *R. purpurascens* cell wall differs in function from cells with papillae in that papillae not only accelerate water uptake, but also accelerate water loss. Pressel *et al.* surmise that unlike the alternating conditions experienced by *R. purpurascens*, constantly flowing aerated water or underhangs where water logging can depress gas exchange select for mosses that are protected from water logging by surface waxes – a condition seemingly quite different from that seen in tracheophytes.

Fluorescence

Fluorescence is seldom mentioned in bryophyte studies. I can remember the excitement of Gisela Nordhorn-Richter when she relayed to me the use of a fluorescent microscope to see propagula in *Pohlia*. It became a great tool for detecting these often obscure structures with UV light.

Following her enthusiasm, I had the opportunity to examine *Fontinalis antipyretica* with a fluorescent microscope and was surprised to find beautiful yellow cell walls and glowing red chloroplasts (Figure 128) – well, the chloroplasts didn't really surprise me, but they certainly made a beautiful image.

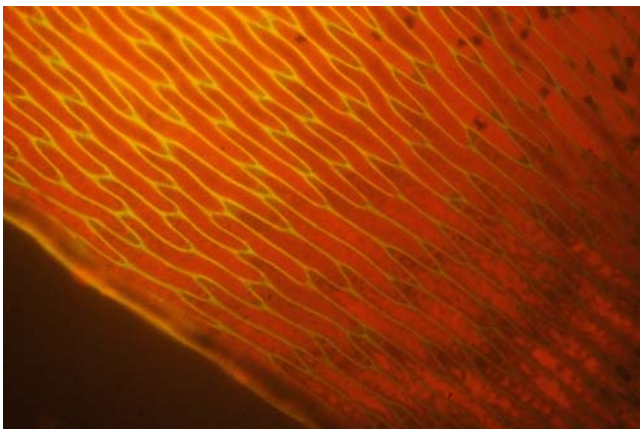


Figure 128. *Fontinalis antipyretica* wall fluorescence. Photo by Janice Glime.

Kroken *et al.* (1996) found that both charophytes and bryophytes have fluorescent cell walls. They suggested that the bryophytes inherited this fluorescence ability from the charophytes, citing evidence from time of production and location. A number of charophytes produce these

resistant cell walls in response to desiccation stress. Furthermore, *Coleochaete* (Figure 129) is the only charophyte known to produce fluorescent tissues at the placental junction in hydrated tissues, induced by sexual reproduction. However, this characteristic is true of all bryophytes tested. Furthermore, in *Sphagnum*, the maternal tissue in the apical portion of the **pseudopodium** (Figure 130) has fluorescent compounds similar to those in *Coleochaete* zygotes. Other known sites of autofluorescence in bryophytes include the sporangial epidermis, spiral thickenings of elaters, rhizoids, and leaves. Kroken and coworkers suggested that this fluorescence represents repeated exaptation. The regulation of deposition has been modified through time, "resulting in a sequence of functions: desiccation resistance and/or microbial resistance in lower charophytes, a role in embryogenesis in *Coleochaete* and embryophytes, and finally, decay resistance in innovative structures that characterize bryophytes, such as rhizoids, sporangial epidermis, and elaters.



Figure 129. *Coleochaete*, the only alga known to produce fluorescent tissues at the placental junction. Photo by Yuuji Tsukii, with permission.



Figure 130. *Sphagnum* with capsule, showing the upper portion of the pseudopodium where fluorescent compounds are produced (arrow). Photo by Vita Plasek, with permission.

Thallus

Liverworts are of two types – thalloid and leafy. The thallus brings its own set of adaptations, with its thickness making possibilities that are not available to the leafy taxa with their one-cell-thick leaves. Among the **xerophytic** (of dry habitats) adaptations are the ability to roll up, shrivel, or fold the thalli, exposing the normally ventral side where red pigments (**anthocyanin**) or hyaline ventral scales (Figure 131-Figure 132) serve to protect the photosynthetic tissue from damage due to exposure to sunlight while dry (Kürschner 2004). The hyaline scales such as those in many *Mannia* (Figure 131-Figure 132), *Riccia* (Figure 133), and *Oxymitra* (Figure 134) species undoubtedly serve to reduce desiccation and provide capillary spaces to facilitate water uptake upon wetting.



Figure 131. *Mannia androgyna* in hydrated condition with reddish edges that characterize the color of anthocyanins on the ventral side. Photo by Michael Lüth, with permission.



Figure 132. *Mannia fragrans* showing curling of the drying thallus; hyaline ventral scales and reddish under surface will soon protect the photosynthetic tissue. Photo by Michael Lüth, with permission.



Figure 133. *Riccia trichocarpa* showing hairs that can reduce water loss and protect the photosynthetic tissue from damage by UV rays. Photo by Jonathan Sleath, with permission.



Figure 134. *Oxymitra incrassata* showing marginal scales. Photo by Chris Cargill, with permission.

The raised cells of the epidermis and the chimney-like hyaline air chambers of some species in *Exormotheca* (Figure 135) may likewise serve as protection from solar radiation and protection from desiccation. Thalli of some species have "windows" (**Fensterthallus**), for example the chimney-like, hyaline air-chambers of *Exormotheca* (Figure 135-Figure 136), like those in the flowering plant family Aizoaceae (for example *Lithops*). These windows provide a covering that helps to reduce the light intensities that reach the photosynthetic layer (Kürschner 2004). The liverwort thallus is thick and nearly semi-circular in cross section. Internally, it has dense assimilatory columns in its air chambers. The column thickness in the liverworts frequently correlates with the degree of insolation.



Figure 135. *Exormotheca welwitschii* in southern Portugal, showing "windows" in the thalli. Photo by Michael Lüth, with permission.



Figure 136. *Exormotheca* sp. thallus showing columnar cells that form the windows to the photosynthetic tissue of the thallus. Photo © Wilhelm Barthlott <lotus-salvinia.de>, with permission.

Liverworts such as *Plagiochasma rupestre* (Figure 137) have hydrophobic wax globules on the thallus surface, making them unwettable. Such waxes keep xerophytic members of the **Marchantiales** from taking up water through the thallus surface, using their pegged rhizoids instead.



Figure 137. *Plagiochasma rupestre*, a thallose liverwort with hydrophobic wax on its surface. Photo by Jan-Peter Frahm, with permission.

Thallus pores may serve as a site of water entry, but a ring of wax around the inner margin of the pore in species

like *Marchantia polymorpha* (Figure 138-Figure 140) serves both to repel water and to make the opening smaller, making it difficult for cohesive water droplets to enter the air chambers of the thallus. Many thalloid species have hydrophobic cuticular ledges around these pores (Ziegler 1987). These waxes protect the air chambers from becoming water-logged (Schonherr & Ziegler 1975; Kürschner 2004).



Figure 138. *Marchantia polymorpha* section of thallus showing pore opening with ridge extending from apical cells of pore. Photo by Wilhelm Barthlott, with permission.

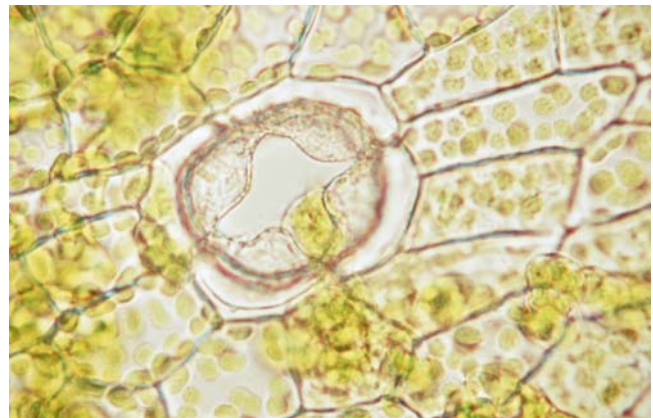


Figure 139. *Marchantia polymorpha* thallus pore opening with ridge. Photo by Wilhelm Barthlott, with permission.

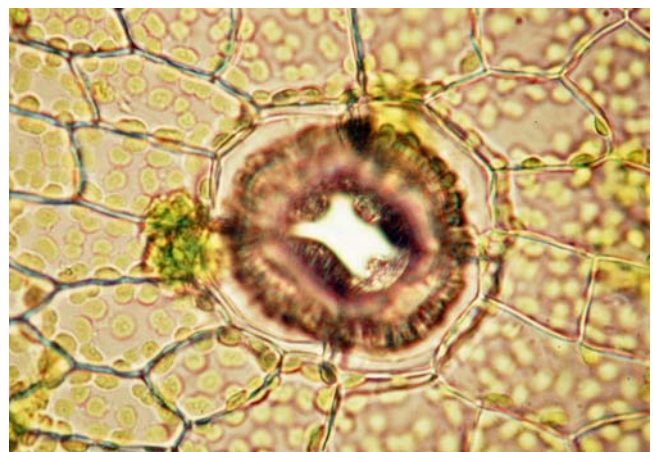


Figure 140. *Marchantia polymorpha* thallus pore opening with ridge that is heavily endowed with wax. Photo by Wilhelm Barthlott, with permission.

Once inside the thallus, we must look for adaptations to obtain sufficient CO₂ and to maintain moisture. For the

thallose liverworts this problem seems to be solved in a manner similar to that of most flowering plants – a ventilated photosynthetic tissue that has stacks of cells one cell wide interspersed within air chambers (Figure 138) (Proctor 2010).

Pigmentation

In physiological studies on animals, it is clear that environmentally induced variation is often adaptive. More arachidonic acid makes membranes more pliable. Non-nucleating proteins prevent ice crystallization. Changes from glucose to glycogen prepare an animal for dormancy. Even physical changes, such as color of fur or feathers, can prepare an animal for a change in seasons. Development of red pigment in *Sphagnum* (Figure 141) and *Fontinalis* (Figure 142-Figure 143) may protect the chlorophyll from high light intensity.



Figure 141. *Sphagnum* showing the red colors that develop in some species when they grow in the sun. Photo by Janice Glime.

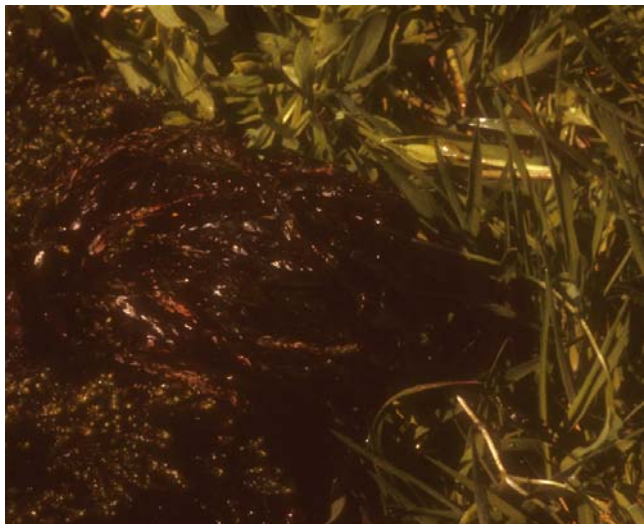


Figure 142. *Fontinalis antipyretica* with red pigments responding to cold spring water and full sun. Photo by Janice Glime.

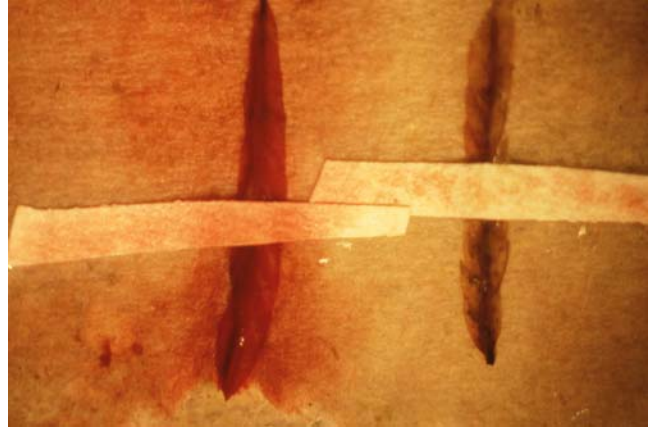


Figure 143. *Fontinalis antipyretica* with red pigments, responding to being out of water, but moist, in bright light. Photo by Janice Glime.

Red pigments in high elevations and alpine regions might serve dual purposes. The red color can protect the chlorophyll and DNA from UV damage, but it could also cause the mosses to absorb heat in their cool climate. The images of *Grimmia elongata* (Figure 144-Figure 145) illustrate the green and red color expressions in this species.



Figure 144. *Grimmia elongata* showing its green form. Photo by Michael Lüth, with permission.



Figure 145. *Grimmia elongata* in Norway, exhibiting its red pigments in the high UV light of the high elevation. Photo by Michael Lüth, with permission.

Some pigmentation may just come along for the ride. For example, phenolic compounds are typically colored, but their primary function can be support or antiherbivory. Such support functions are most likely for structures like the costa (Figure 146) or stem rigidity (Figure 147), but they also occur in many leaf borders (Figure 43).

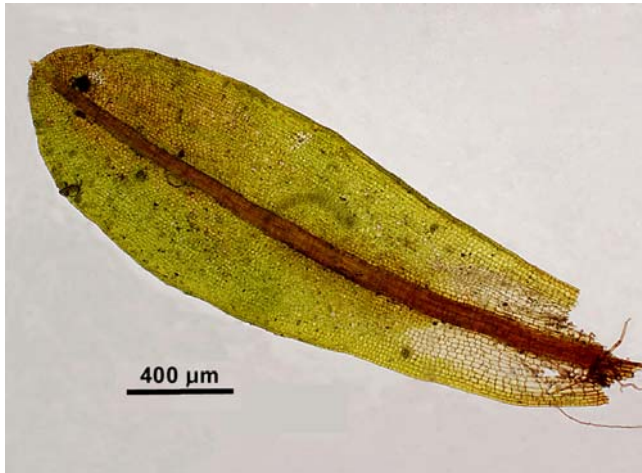


Figure 146. *Syntrichia inermis* leaf showing dark color in costa. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

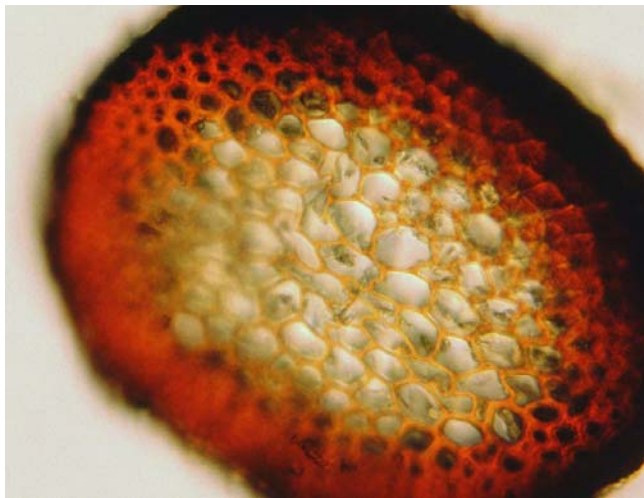


Figure 147. *Fontinalis dalecarlica* stem section showing dense coloration in the cell walls. Photo by Janice Glime.

Gender

Zander (Bryonet 8 May 2012) suggested that the presence of only males in a population would have the adaptive advantage of conserving photosynthate by the lack of necessity for producing sporophytes. Thus dioecy in dry habitats might be an adaptation to conserve photosynthate. But Stark has reported that in many desert populations the males are absent. Nevertheless, this principle would operate whether the population was male or female. On the other hand, monoecy provides advantages in a moist or otherwise less stressful habitat where there is sufficient energy for producing sporophytes.

Adaptive value of gender expression was discussed in detail in Chapters 3 and will not be discussed further here.

Wound Response

If you are a plant, what you do when you get damaged may have important effects on the future of your species. And if you live in fast-flowing water (Figure 148), that damage is a certainty. Some species are adapted to take advantage of the wounds; others merely protect themselves; some (perhaps most bryophytes) do both. The advantage for bryophytes – a means for dispersing and making new colonies.



Figure 148. *Cinclidotus danubicus* habitat, illustrating the power of the water. Damage to leaves can be significant during high-water events. Photo by Michael Lüth, with permission.

We have limited understanding of the means of protection. One study on the biochemical response is that for *Marchantia polymorpha*. When wounded, *Marchantia polymorpha* (Figure 149) produces highly volatile 8-carbon compounds including (R)-1-octen-3-ol and octan-3-one (Kihara *et al.* 2014). These emissions occurred within 40 minutes of the wounding. The importance of arachidonic acid and/or eicosapentaenoic acid was demonstrated by the weak or absent response of the volatiles. In completely disrupted thalli, only minimal amounts of octan-3-one were produced, whereas the greatest amounts were produced in partially disrupted thalli, compared to undisturbed thalli. This suggests signalling from the disrupted cells that initiates the production of octan-3-one in the undisturbed cells.



Figure 149. *Marchantia polymorpha* with an isopod – a potential herbivore. Herbivory and other wounds can stimulate production of highly volatile compounds in this liverwort. Photo by Walter Obermayer, with permission.

Croisier *et al.* (2010) found a variety of responses in the bryophytes they surveyed. Instead of the predominant C8 volatiles, they found a variety of C5, C6, C8, and C9 volatiles in 23 mosses tested. These are **oxylipins** – metabolites derived from oxidative fragmentation of polyunsaturated fatty acids. Both C18 and C20 fatty acids serve as the precursors for the volatile oxylipins that respond to mechanical wounding of mosses. These oxylipins are important hormonal regulators and defense compounds in plants. In liverworts and hornworts, oxylipin production was less pronounced than in the mosses.

This still leaves us with the ecological question of how these volatiles protect the species. Do they deter herbivores, as do many volatiles in tracheophytes? The *Marchantia* story suggests they are inducible. Do they protect against fungal attack? (Fungal attack will be covered later in a chapter on fungal interactions.) Do they play any role in dedifferentiation and regrowth? Do they stimulate the production of rhizoids or protonemata often seen at wound sites? This would seem to be a fertile area of research for understanding hormonal interaction and control of development in bryophytes.

Summary

Bryophytes have a simple structure. That does not mean they have not advanced morphologically. Their stems may have conducting cells, have various phenolic compounds in the cell walls, or be covered with paraphyllia, rhizoids, or tomentum. The leaves may have borders, marginal teeth, lobes, hair tips, costae, lamellae, or keels. The leaf cells may be short and nearly isodiametric (often with thick walls), larger hexagonal cells with thin walls, or elongate narrow cells. These cells may have waxes, papillae, or be swollen. These structures seem to be adaptations to habitats ranging from aquatic to desert.

Aquatic bryophytes that do not spend much time out of water generally lack papillae, have elongate narrow cells, and lack conducting cells in the stems. They may have strong stems with colored cells walls from phenolic compounds, protecting them against moving water and suspended solids. At the other extreme, xerophytic bryophytes are often papillate, have thicker waxes, are reduced in size, and have mechanisms of curling up while dry and expanding when wet. Specialized cell walls, lamellae, and marginal teeth may provide mechanisms to increase photosynthesis while preventing water logging. Hair tips can scatter high light, absorb water, or reduce drying. Pigments can protect bryophytes from high light intensities, especially when low temperatures slow photosynthesis or the plant is dormant due to high temperatures.

Leafy liverworts may be able to hold water droplets with their lobes and teeth. These structures could also serve to deter herbivores. The thallus can have windows to direct light and protect the photosynthetic cells, be protected by waxes and scales, have thallus pores that open and close, permitting gas exchange while preventing internal water logging.

These adaptive value of bryophyte structures are largely speculation, hypotheses waiting to be tested.

Acknowledgments

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CHAPTER 4-13

ADAPTIVE STRATEGIES: SPECULATIONS ON SPOROPHYTE STRUCTURE

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CHAPTER 4-13

ADAPTIVE STRATEGIES: SPECULATIONS ON SPOROPHYTE STRUCTURE



Figure 1. *Bryum argenteum* capsules, representing the sporophyte generation. Photo by Dick Haaksma, with permission.

SPOROPHYTE

The sporophyte is that generation seen as a stalk and capsule (with an unseen foot) perched on top of the gametophyte. During young stages the sporophyte will bear a gametophyte **calyptra** that influences its development.

Vanderpoorten *et al.* (2002) conceded that sporophyte traits in the **Amblystegiaceae** (Figure 2) are more "labile" than previously thought, warning that an understanding of that plasticity is necessary to prevent giving the traits undue emphasis in classification systems. In fact, many sporophyte characters are strongly correlated with habitat conditions.



Figure 2. *Hygrohypnum luridum* (Amblystegiaceae) capsules in the wet zone. Photo by Michael Lüth, with permission.

Calyptra

The calyptra is not part of the sporophyte. Rather, it is developed from the archegonium after the embryo becomes sufficiently large to force the splitting of the archegonium. The upper portion of the archegonium remains on the developing sporophyte and becomes the calyptra. Its function after it becomes a calyptra influences the sporophyte development, so it is perhaps better discussed here in its influence on the sporophyte, rather than under the topic of gametophyte.

As discussed in the chapter on development, the calyptra creates an environment in which the capsule develops, and it influences the shape of the capsule. If the calyptra is removed too early, the capsule may fail to develop. Split calyptrae (Figure 3) can result in uneven development, leading to curved capsules. It would be easy to design experiments to compare effects of removal or split calyptrae, including effects of timing, on a variety of species representing different groups of bryophytes. The results could be quite interesting.



Figure 3. *Pylaisia polyantha* capsule with split calyptra that can cause the capsule to develop asymmetrically if it splits early enough in development. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

But is there any role for the structure of the surface of the calyptra?

Hairs

Lloyd Stark (Bryonet 8 May 2012) observed that the hairs on the calyptra of *Forsstroemia* (Figure 4) result when paraphyses in the female inflorescence resume extension in length upon fertilization. One hypothesis for this trait is that such long hairs help keep the relative humidity high within the perichaetial leaves, thus acting to retard the rate of desiccation for the developing embryo. Then, when the sporophyte is mature, these hairs are retained on the calyptra. I haven't followed the development, but the hairs of at least some taxa seem too large to be just a lingering of the archegonial hairs, suggesting that they enlarge as the calyptra enlarges,

requiring energy and resources. If they continue to extend as the calyptra develops, then there may be some advantage that would favor that prolonged use of energy.



Figure 4. *Forsstroemia trichomitria* with capsules. Photo by Bobby Hattaway (www.discoverlife.org), through online permission.

There appear to be two kinds of hairs, "true" hairs and undeveloped archegonia. In *Fontinalis*, the calyptral "hairs" develop from aborted archegonia (Figure 5) whose eggs were presumably not fertilized (Glime 1983). This results in a small number of hairs near the base of the calyptra.



Figure 5. Aborted archegonium (SEM) on calyptra of *Fontinalis squamosa*. Photo by Janice Glime.

Neil Ellwood (9 May 2012) recounted a story about benthic filamentous Cyanobacteria that may have some relevance for calyptra hairs. These cyanobacterial hairs had no photosynthetic capacity, but they had high phosphatase activity. They were produced at times of phosphorus stress. He suggested that one possibility for the hairs of *Orthotrichum* (Figure 6) might aid in the uptake of nutrients from the moisture trapped among them. As a follow-up to this discussion, Johannes Enroth (Bryonet 9 May 2012) suggested two hypotheses:

1. Hairy calyptrae are more common in nutrient-poor environments.
2. Hairy calyptrae are larger than hairless ones in relative as well as absolute terms.



Figure 6. *Orthotrichum cupulatum* showing hairs on the calyptra. Photo by Jan-Peter Frahm, with permission.

Neil Ellwood (Bryonet 10 May 2012) suggested testing hypothesis number 1 by staining the calyptra with BCIP/NBT (colored stain) or ELF97 (fluorescent) with and without hairs on medium with and without P limitation. The P limitation can be enhanced by augmenting the N concentration. This should be supported by testing tissue levels of N and P. He points out that bacteria, Cyanobacteria, green algae, and diatoms are known to use extensions in response to nutrient limitation. In the biofilm diatom *Didymosphenia*, these enzymes are pushed into the stalks, an extension of the cells. The continuation of this practice in bryophytes might be expected. It is an interesting idea that has never been tested. What other bryophyte structures might serve such a function? Leaf hairs? Stem tomentum?

But Claudio Moya Delgadillo (Bryonet 9 May 2012) raised an interesting point. When the archegonium breaks away from the underlying stem to ride atop the developing sporophyte (forming the calyptra), the capsule has not yet expanded. Hence whatever growth occurs in the calyptra must come from contact with the expanding urn of the capsule – or from its own activity? This raises the question of just when the hairs expand and where they get the energy to do it.

Capsules

Ken Kellman (Bryonet 8 May 2012) recounts his experience searching for bryophytes in pouring rain. He noticed numerous bryophyte species had droplets of water sequestered by their capsules (Figure 7) and was struck by

the need for a hydrophilic surface chemistry to accomplish that phenomenon. Whatever their function, it is likely that different capsule shapes and sizes also affect the ability to hold the water drops. Capsules of *Orthotrichum* (Figure 6) were an exception to holding water and Kellman suggested that perhaps the hairs on the calyptrae helped to disperse the water droplets. On the other hand, perhaps the hairs on the calyptrae help to discourage foraging by slugs that tend to eat capsules.



Figure 7. *Bryum capillare* showing water drop clinging to capsule. Photo © Stuart Dunlop <www.donegal-wildlife.blogspot.com>, with permission.

Capsule Structure

Like Vanderpoorten *et al.* (2002) for the *Amblystegiaceae*, Rose *et al.* (2016) concluded that capsule shape is driven by differences in physiological demands in diverse habitats. Furthermore, they found that sporangium shape is a convergent character associated with habitat type. In fact, "many shifts in speciation rate are associated with shifts in sporangium shape across their 480 million year history."

Stomata

Location, Structure, and Number

Stomata, those openings between a pair of guard cells that are familiar structures of tracheophyte leaves, are also present in the sporophytes of many bryophytes (Paton & Pearce 1957). They are absent among the *Marchantiophyta* (Figure 10) (Crum 2001), but seem to be homologous in the *Bryophyta* (Figure 8) and *Anthocerotophyta* (Figure 9) (Renzaglia *et al.* 2000; Ligrone *et al.* 2012), but apparently with somewhat different selection pressures at play and sometimes a rather different role from that in tracheophytes. Despite their rather widespread presence, they are absent in several highly organized but unrelated genera of bryophytes (Paton & Pearce 1957).

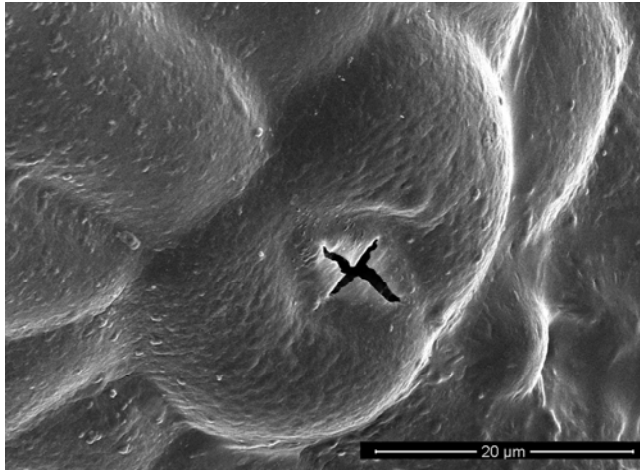


Figure 8. *Physcomitrella patens* sporophyte stomata SEM. Photo courtesy of Jeff Duckett and Silvia Pressel.

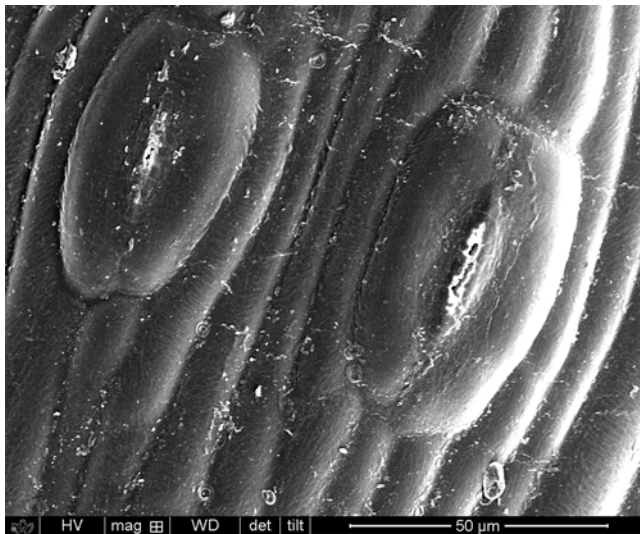


Figure 9. *Anthoceros punctatus* sporophyte stomata SEM. Photo courtesy of Jeff Duckett and Silvia Pressel.



Figure 10. Liverwort *Fossombronia* cf. *caespitiformis* capsule showing its ability to repel water. Liverwort capsules lack stomata. Photo by Andras Keszei, with permission.

In some mosses, the guard cells are round in cross section, have thick walls, and do not open and close (Ziegler 1987). These occur in species with reduced photosynthetic tissue in the capsule. These have been considered to be evolutionarily reduced, not primitive. It is interesting that, unlike tracheophytes, mosses lack subsidiary cells associated with the guard cells, and the guard cells are larger than the surrounding epidermal cells (Figure 11), two characteristics distinguishing them from the stomatal apparatus of tracheophytes.

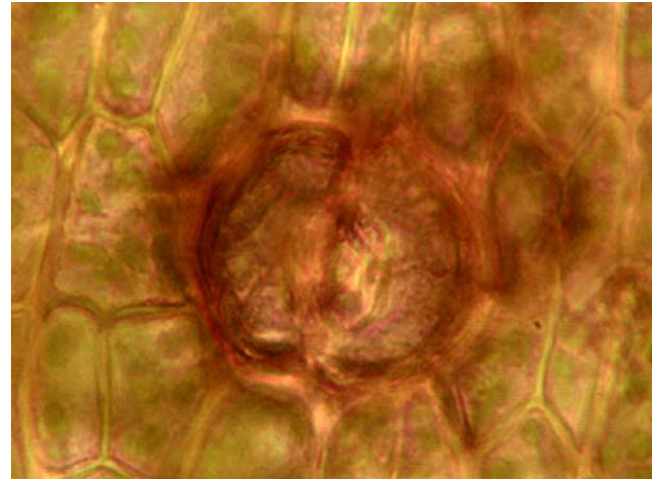


Figure 11. *Orthotrichum affine* stoma showing two guard cells, no subsidiary cells, and larger size of guard cells compared to epidermal cells. Photo by Malcolm Storey, through Creative Commons.

Paton and Pearce (1957) surveyed the stomata of British bryophytes and found that most of the stomata were 20–45 μm wide, but ranged 20 μm to 60 μm or more and were typically 70 μm long or more. The guard cell walls, typically two, may be thick or thin, and the stomata may be round or elongate (Figure 17). Generally the long axis of the stoma is parallel with the long axis of the capsule.

Stomata number varies widely and depends largely on the size of the capsule, with small capsules of *Pleuridium* (Figure 12) and *Acaulon* (Figure 13) having only four and *Polytrichum* (Figure 14) and *Philonotis* (Figure 15) having over 200 (Paton & Pearce 1957; see also Egunyumi 1982 for tropical African mosses). Most, however, at least in Great Britain, have 15 or fewer.



Figure 12. *Pleuridium subulatum* showing small capsules that have only 4 stomata. Photo by Kristian Peters, with permission.



Figure 13. *Acaulon muticum* with small capsules hidden within the perichaetial leaves. Photo by Jan-Peter Frahm, with permission.

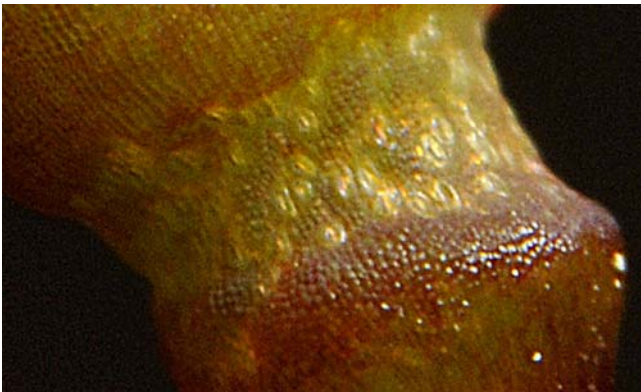


Figure 14. *Polytrichum* stomata at neck of capsule. This genus can have more than 200 stomata. Photo by George Shepherd, through Creative Commons.



Figure 15. *Philonotis revoluta* capsules, a genus with more than 200 stomata on the capsule. Photo by Zen Iwatsuki, with permission.

One might expect the level of the guard cells relative to the capsule surface to be of adaptive significance, and these may be slightly raised (Figure 16), level with the epidermis (Figure 17), or sunken (Figure 18), but most are level with the epidermis (Paton & Pearce 1957). Paton and Pearce (1957) concluded that there was no relationship between sunken stomata and a dry habitat. Only in *Polytrichum* (Figure 16), where the stomata are in deep, narrow grooves in species from dry habitats and are shallow in those from wet habitats, is there a suggestion of adaptive location (Bünger 1890).

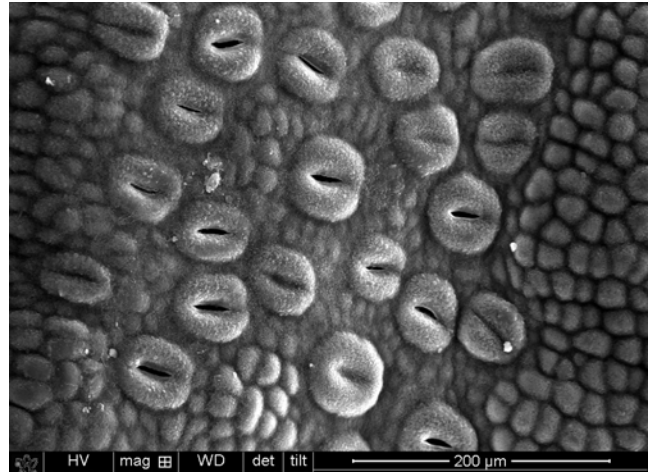


Figure 16. SEM of *Polytrichum juniperinum* stomata at capsule base. Photo courtesy of Jeff Duckett and Silvia Pressel.

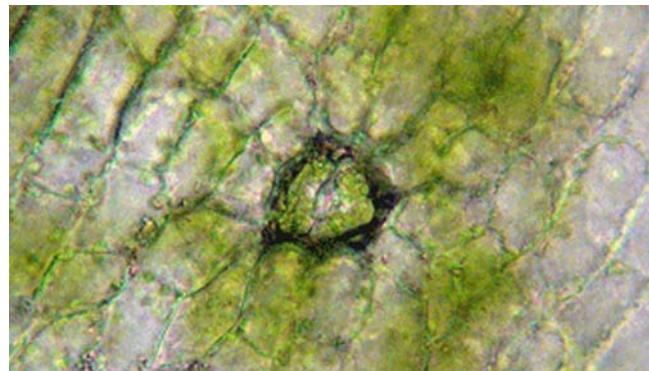


Figure 17. *Orthotrichum pusillum* surface stoma. Photo by Bob Klips, with permission.

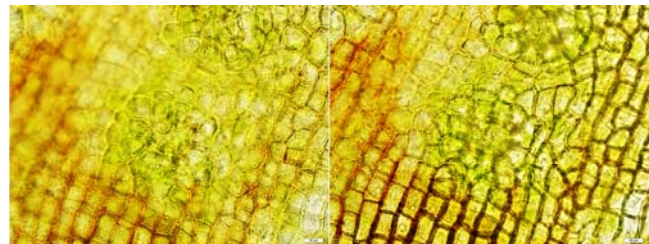


Figure 18. *Orthotrichum anomalum* showing sunken stomata. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Stomatal Functioning

The real puzzle came with observations by Haberlandt (1886) on the mechanism of closing the guard cells. Unlike the leaf tissue of tracheophytes, the tissue adjoining the guard cells of moss capsules is very thick and the guard cells cannot bulge into it. Using *Plagiomnium cuspidatum* (Figure 19), Haberlandt showed that only the ventral wall of the guard cell is capable of movement. This causes the width of the guard cell to increase and the depth to decrease as the turgor decreases, closing the pore across the middle. But this meant that the length and width of the stoma remained the same whether it was open or closed. Bünger (1890) made similar observations regarding the behavior in *Polytrichum* (Figure 16), but he found in addition that the upper and lower ridges of the guard cells would come together to close the stoma, reminiscent of the action of the tier of pores in the thallus of *Marchantia* (see Chapter 4-

12). But Paton and Pearce (1957) revealed a caveat for these observations. They were done by immersing the capsules in glycerine, a typical mounting medium at that time. The glycerine kills the cells, so these results might not be indicative of what would happen naturally.



Figure 19. *Plagiomnium cuspidatum* capsules with guard cells that close in response to increased turgor. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Adaptive Significance

Small numbers of small stomata are typical among species of dry habitats. Variations in stomata density in at least some **Polytrichaceae** (Figure 14, Figure 16) can depend on the environment, with those species in moist habitats having more stomata per mm² (Szymanska 1931). Paton and Pearce (1957) found the same trend among the wider sampling of British bryophytes. Because the stomata are usually restricted to a very small area of the capsule, usually below the level of the spore mass and often located on the apophysis and neck of the capsule (Figure 14), their restricted locations and small numbers make them difficult to count accurately. It is interesting that Paton and Pearce found a positive correlation between length of seta and number of stomata, a relationship also observed by Egunyumi (1982) for tropical African mosses. But as was seen in subchapter 4-7, the length of the seta is diminished in many taxa of dry habitats. And one might suppose that if capsules are immersed in perichaetial leaves, stomata would be of little value. Indeed, in such taxa as *Pleuroidium* (Figure 12) and *Acaulon* (Figure 13), there are only four stomata, but this also correlates with the small capsule size.

It appears that the stomata may serve in water regulation to photosynthetic tissue of the capsule (Paton & Pearce 1957). The stomata seem to be confined to green portions of the capsule, and larger assimilatory portions had more stomata (Haberlandt 1886). Bünger (1890) interpreted the stomata at an older stage to have a waxy plug and thus assumed that the stomata were no longer required because the tissue had ceased being assimilatory. Haberlandt made the interesting observation that species with sunken stomata had a poorly developed assimilatory region. He also demonstrated that the guard cells could open and close the stoma, depending on their turgor.

Vaizey (1887) described the movement of water through the sporophyte, with uptake by the foot, transport

up the seta, and transpiration through the stomata, suggesting that they could close to minimize the effects of drought. Perhaps it is also important for them to be open to facilitate this upward movement of water and solutes. Blaikley (1932) added credence to this transpiration interpretation by putting vaseline in the stomatal groove of *Polytrichum commune* (Figure 20) and found that the transpiration rate fell to one third of the original rate. However, Paton and Pearce (1957) caution that this experiment also blocked the cuticle, and that the cuticle is known to have considerable transpiration.



Figure 20. *Polytrichum commune* capsules. Photo by Michael Lüth, with permission.

Paton and Pearce (1957) set out to demonstrate the effects of the environment on the closing of the guard cells. They reasoned that they could not examine opening because older guard cells were permanently closed. Their results are interesting:

1. dry vs moist, 24-hr or 16-hr light or continuous dark: stomata tended to be open in moist, closed in dry conditions
2. dry vs moist, 4°C & 35°C: stomata usually remained open
3. dark for 24 & 48 hr, then light for 1/2 & 1 hr: stomata mostly open
4. dark for 48 hr, then CO₂-free atmosphere for 1-24 hr darkness: always some open stomata
5. 1, 3, 6, 12, 24-hr exposure to each combination of light & dark, dry, very dry, and normal air, CO₂-free & 5% CO₂: open stomata in all conditions

When they did a new set of experiments, including some new species, results were similar, with the only closure occurring when the capsules dried out (Paton & Pearce 1957). In one experiment they dried the capsules for 3-4 days, then soaked them overnight, and some of the stomata opened. In their final experiment, they placed *Bryum bicolor* (Figure 21) capsules on a glass slide under the microscope, allowed them to dry, and observed the shrivelled epidermis and closed stomata. When they added water, the epidermal cells again swelled and the stomata

opened. After repeating this response with other species, they concluded that the stomata are capable of opening and closing in response to the water content of the cells.



Figure 21. *Bryum bicolor*, a moss in which stomata close and open in response to drying and rewetting. Photo by Jonathan Sleath, with permission.

Sphagnum - As you have seen in the discussion of the **Sphagnum Explosion** in subchapter 4-9, the stomata can, at least in that genus, play a role in capsule drying, leading to dehiscence. These stomata do not respond to potassium levels, but rather respond to the hormone ABA (Chater *et al.* 2011). Nevertheless, they respond to environmental signals in the same way as guard cells of tracheophytes. This leaves us with the question of whether the stomata have any role in dehiscence in taxa other than *Sphagnum*.

Interpretation of the role of stomata is confused by the rather odd distribution among the taxa. They are present in most of the **Dicranaceae** examined, but absent in *Campylopus* (Figure 22) (Paton & Pearce 1957). They are likewise absent in several very short, ephemeral taxa with cleistocarpous capsules [*Acaulon* (Figure 13), *Micromitrium* (Figure 23)], but they are present in the ephemeral, cleistocarpous *Ephemerum* (Figure 24). There seems to be a trend to absence in aquatic taxa: *Octodiceras* (Figure 25), *Cinclidotus* (Figure 26), *Fontinalis* (only 1 species examined; Figure 27). But Paton and Pearce found both stomate and non-stomate capsules among epiphytes and forest floor species, making any habitat conclusions very tenuous.



Figure 22. *Campylopus nivalis*, a species of **Dicranaceae** with no stomata. Photo by Michael Lüth, with permission.



Figure 23. *Micromitrium tenerum*, a species with cleistocarpous capsules and no stomata. Photo by Amelia Merced, through Creative Commons.



Figure 24. *Ephemerum minutissimum*, a tiny ephemeral species with stomata. Photo by Jan-Peter Frahm, with permission.



Figure 25. *Fissidens fontanus*, a species that tends to lack stomata. Photo by Michael Lüth, with permission.



Figure 26. *Cinclidotus fontinaloides* with capsules that lack stomata and have the capsule base buried in perichaetial leaves. Photo by Michael Lüth, with permission.

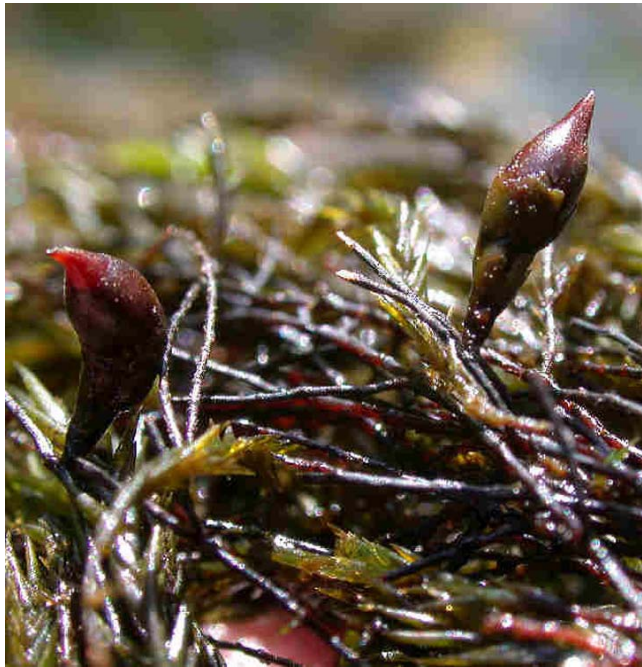


Figure 27. *Fontinalis dalecarlica* with capsules, member of a genus where at least one species lacks stomata. Photo by Janice Glime.

The presence of the stomata should relate to their function if evolutionary processes have had sufficient time to select against those that are less fit. Let's examine this relationship in the **Polytrichaceae**. Haig (2013) reports that the stomata are prevented by the calyptra from functioning in transpiration until that calyptra is pushed upward sufficiently far for the stomata to be exposed (Haig 2013). That raises an interesting question regarding certain members of the **Polytrichaceae**. How can stomata function at all in transpiration in species where the calyptra covers the entire capsule until the capsule reaches maturity? One would expect the transpiration function to be most important during the early stages when photosynthesis is occurring in the capsule.

In the **Polytrichaceae** stomata are absent in *Atrichum* (Figure 28), *Pogonatum aloides* (Figure 29), *P. urnigerum* (Figure 30), and *Polytrichastrum alpinum* (Figure 31), but present in *Oligotrichum* (Figure 32), *Polytrichum strictum* (Figure 33), *Polytrichum commune* (Figure 20), and numerous (nearly 200) in *Polytrichastrum formosum*

(Figure 34) (Paton & Pearce 1957). It appears that the gametophyte and sporophyte may be working at cross purposes here. If indeed the calyptra prevents the stomata from functioning, then why are they present in *Polytrichum strictum* (Figure 33) and *P. commune* (Figure 20) that both have long calyptrae that still cover the whole capsule at maturity, but absent in *Atrichum* (Figure 28) and *Polytrichastrum formosum* (Figure 31) that have abbreviated calyptrae? Is this a gametophyte (calyptra) trait where the coverage of the calyptra is important to the developing capsule in the *Polytrichum* species? This suggests that the stomata of the sporophyte are not sufficiently detrimental, if at all, to cause elimination of that combination. This is perhaps a good illustration of the differing and sometimes conflicting selection pressures on the two generations, with the gametophyte pressure taking precedence here.



Figure 28. *Atrichum undulatum* with capsules and short calyptrae – a genus that lacks stomata. Photo by Martin Hutten, with permission.



Figure 29. *Pogonatum aloides*, a species lacking stomata in the capsule and with the calyptra covering most of the base of the capsule. Photo by Michael Lüth, with permission.



Figure 30. *Pogonatum urnigerum*, a species lacking stomata in its capsules. Photo by Janice Glime.



Figure 33. *Polytrichum strictum*, a species of **Polytrichaceae** with stomata, but with the capsule covered at maturity. Photo by Michael Lüth, with permission.



Figure 31. *Polytrichastrum alpinum*, a species that lacks stomata but has the lower part of the capsule exposed. Photo by Hermann Schachner, through Wikimedia Commons.



Figure 34. *Polytrichastrum formosum*, a species of **Polytrichaceae** with stomata. Photo by Michael Lüth, with permission.



Figure 32. *Oligotrichum hercynicum*, a species of **Polytrichaceae** with stomata – and an exposed lower half of the capsule. Photo by Michael Lüth, with permission.

Ligrone *et al.* (2012) considered the stomata to be a sporophyte innovation with the "possible ancestral functions of producing a transpiration-driven flow of water and solutes from the parental gametophyte." If we consider the importance of stomata in tracheophytes, we know that they provide the end of the transpiration stream that is needed to bring water and minerals to the top of the plant. Since bryophytes take in most of their water through their leaves, this at first might seem like an unnecessary function. But the stomata are not in leaves, they are above the leaves in the sporophyte. And the sporophyte needs to get nutrients, hormones, and possibly even water from the leafy gametophyte. The seta can serve as a capillary organ to help move these materials, but the open stomata could increase this movement in the same way it does in tracheophyte leaves. This would fit with the absence or small numbers of stomata in sessile capsules and likewise in submersed capsules. But we have no experimental evidence to support this hypothesis.

But Ligrone *et al.* (2012) added a second function - facilitating spore separation before release. This could fit with some of the other theories discussed here, particularly the role of drying in the *Sphagnum* capsule (Figure 35). Drying would help the spores to separate. But would the movement of air, like stirring the pot, provide any facilitation worthy of note?



Figure 35. *Sphagnum plumulosum* showing swollen capsule with operculum, dry compressed capsules, and capsules that have lost their opercula. Photo by David T. Holyoak, with permission.

It is interesting that in mosses the stomata occur only on the sporophyte and in most cases are restricted to that part of the capsule where most of the photosynthesis occurs (Ziegler 1987). This correlation supports the concept of stomata providing a site for CO₂ exchange during the early, photosynthetic stages of capsule development. Figure 22-Figure 33 illustrate the degree of capsule coverage by the calyptra in several species. Those species that do not have stomata in the capsules have a thin capsule epidermis, apparently providing adequate CO₂ exchange.

We are still left with the question of how stomata relates to capsule dehiscence and dispersal. Although the research on *Sphagnum* suggests that the stomata (Figure 36) might play a role in rapid drying of the capsule, leading to dehiscence, there appear to be no data, either observational or experimental, to test this role in other bryophytes. We might even conclude that the wax plugs and other evidence of lost function discussed above (see Stomatal Functioning) would preclude such a function in non-*Sphagnum* capsules. Nevertheless, there could be at least some species in which this function is important. And the absence of stomata in some of the cleistocarpous capsules and some of the aquatic capsules, where they would be of little value might suggest that such a function is being lost where it is not needed. But then that can also be said for its function in capsule transpiration. We need experimentation on a wide range of capsules. And we need to remember that they may serve both functions.

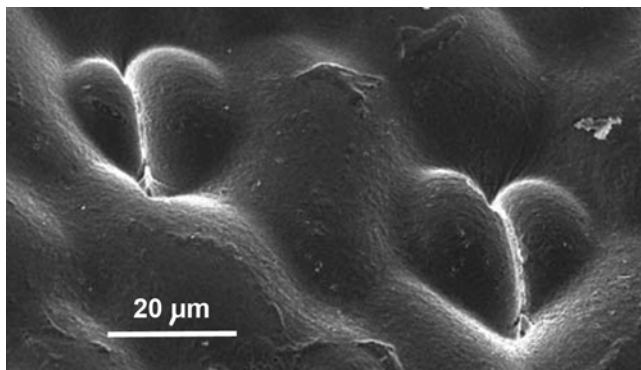


Figure 36. Non-functional stomata of a mature *Sphagnum* capsule. Photo courtesy of Jeff Duckett and Silvia Pressel.

But all of this discussion has been about the Bryophyta. How do the guard cells function in the **Anthocerotophyta** (Figure 37)? What is their role in those horn-shaped sporophytes where dehiscence is continuous and results from splitting that starts at the top and works downward? How can stomata help a sporophyte that is young at the bottom with new spores being produced when the other end of the capsule is wide open? Are they left-overs from functions in their ancestors, or do they have a role we have not even imagined yet?



Figure 37. *Anthoceros agrestis* showing involucre at base and elongate capsule. Photo by Jan-Peter Frahm, with permission.

Ziegler considers these hornwort stomata to be true stomata, functioning like tracheophyte guard cells with a substomatal chamber where photosynthetic tissue resides. Raven (2002) suggests one possibility for their importance – that decreasing levels of CO₂ in the environment required special adaptations to maintain sufficiently high levels of CO₂ for photosynthesis. This makes sense for the hornwort stomata that are present at the base of the sporophyte in the young and dividing tissue. The admission of CO₂ through the stomata would permit higher photosynthesis in the part of the sporophyte that needs it.

Duckett *et al.* (2010) consider the hornwort stomata (Figure 38) to function as they do in *Sphagnum* – to facilitate drying of the capsule interior so that the spores can be dispersed, a suggestion made earlier by Lucas and Renzaglia (2002). They support this conclusion by the determination that the stomata open only after they have emerged from the involucre, and that they remain open thereafter. Furthermore, those "air-filled" spaces inside the stomata are initially filled with mucilage and only become air spaces after drying commences.

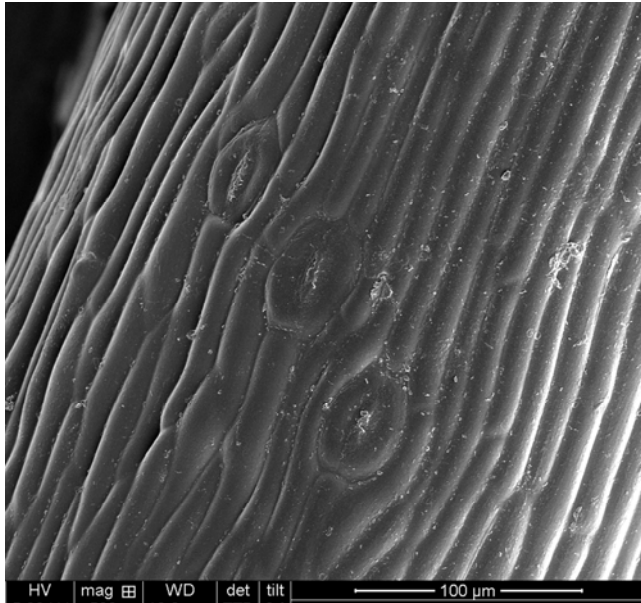


Figure 38. SEM of *Anthoceros punctatus* sporophyte showing stomata. Photo courtesy of Jeff Duckett and Silvia Pressel.

Hornwort Capsules

The hornwort capsules are unique among bryophytes in having a basal meristem. This means that the tip of the capsule is mature first, splits open first, and disperses spores first. It also means that while the tip is dispersing spores, the base continues to produce them. This is certainly an advantage for producing and releasing spores over a longer period of time while at the same time keeping the developing spores near the nutrient sources available from the gametophyte.

But are there other advantages? Roberto Ligrone (Bryonet) suggested that it might be an adaptation to herbivory on the sporophyte, much like grass grows at the base and survives the herbivory of large grazing mammals.

Are Bryophytes Slow to Evolve?

Their small size and seeming lack of complexity has led us to ask if bryophytes have a slow rate of change and consequent evolution. First, Ann Stoneburner and Robert Wyatt have shown that the rate of bryophyte evolution/genetic change has been as rapid as that in tracheophytes. But, as we usually conclude, the morphological expression of this evolution appears to be more limited. Hence, we must look for the expression of this evolution elsewhere. Evolutionary treatises designed for the lay public tend to overlook the fact that evolution is not just about morphology. That is only its most obvious expression. Bryophytes have been "stuck" with one evolutionary problem that has limited their morphological diversity – they lack true lignin. With this structural compound absent, bryophytes cannot accomplish great height due to lack of support. Proctor (2010) contends that bryophytes are simply too small to have the sorts of complexities developed by tracheophytes. Bryophytes have a plant body 100X smaller and a millionth the volume of tracheophytes. One could, therefore, argue that they are

limited by their small size that prevents them from developing great complexity.

To consider their size "limitation," let us consider the historical fate of the horsetails and lycopods. During the dinosaur days, these groups were represented by tall plants – 30 feet or more, with leaves 3 feet long. Those long leaves were serviced by only one vein down the center. Hence, competition for water with emerging plants that had branched veins (ferns, conifers, ultimately flowering plants) most likely put them at a disadvantage. One could argue that their "answer" to that competition was to become small. To avoid being teleological, we can consider that only the small members (perhaps newcomers) survived the competition and drying of habitats.

But bryophytes, in a world where insects were speciating at a phenomenal rate, faced another serious problem. Their slow growth rates made them very vulnerable when attacked by hungry herbivores. Hence, those species that were conspicuous survived best if they were endowed with secondary compounds that discouraged herbivory. And many researchers have described hundreds, perhaps thousands, of secondary compounds. Many of these serve both to discourage herbivory and to prevent disease. These special endowments could permit bryophytes to survive, grow slowly, take advantage of their asexual reproduction to propagate and spread, tolerate cold in winter as C3 plants insulated from extreme cold by snow, and avoid being wiped out by hungry animals, especially right after snowmelt when food is scarce and animals are hungry.

Nevertheless, all these factors favoring smallness and simplicity still seem to evade the question of why they lack structural complexity. Many bryophytes have adapted a strategy of horizontal growth. In that case, support would not seem to be an issue. Why are there no larger structures on these, either above or below ground? What is it that maintains a relatively slow growth rate? To say that their limited photosynthetic tissue prevents them from growing faster would seem to be circular reasoning. (Sorry, Richard, I actually like your argument that the limited photosynthetic tissue limits them, but why has it stayed limited?)

As pointed out by all our contributors to Bryonet thus far, the bryophytes have "found" a group of niches in which they thrive. They are often in situations where many other plants could not thrive, and in some cases the bryophytes are necessary for other plants to become established. Perhaps the bryophytes, or some of them, have "limiting genes" that restrain their growth rates. Gerson (1972) showed that a diet of certain bryophytes could prevent the mite *Ledermuelleria frigida* from reproducing. Perhaps at least some bryophytes have highly conserved genes (e.g. near the centromere) that do a similar thing by inhibiting their own growth.

Let's consider the alternatives to the current bryophyte strategy. Diego Knop Henriques (Bryonet 8 February 2011) expressed his opinion that "the very simplicity of bryophyte structures rendered them one of the greatest physiological abilities to survive all those millions of years: the poikilohydrysm." Although the flowering plants are the most diverse plant group on the planet, the bryophytes are second. Furthermore, there are few habitats where no bryophyte can grow. (It is of note that the ocean is one of

them.) Their distributions are generally wider than those of flowering plants, attesting to their good dispersal ability. They have incredible abilities to survive a wide range of conditions, to come back to life from ages past, and to avoid being devoured by advancing herbivores. Diego Knop Henriques sums up his perspective as "simplicity + effectiveness in physiological and reproductive strategies may be the evolutionary way bryophytes followed, while great complexity + intense investments in defenses and specializations in several ranks were one of the paths flowering plants and others followed to struggle for survival. Structural complexity was not a necessary condition for bryophytes to diversify and maintain themselves as one of the living branches of The Tree of Life."

What might be lost if bryophytes were larger or more morphologically diverse? Could they still develop easily from fragments if they had large, showy reproductive organs or complex leaves? Would thick cuticles make regeneration from a leaf impossible, or at least improbable? Would a faster growth rate be at the expense of secondary compounds that prevent herbivory? I agree, they seem to be well adapted for their circumstances, and I think they will outlive most or all other plant groups under radically changing conditions of the planet.

Rod Seppelt (Bryonet 8 February 2011) reminded us of the Baas-Becking hypothesis, "Everything is everywhere, but the environment selects." He reminds us of the morphological diversity in genera such as *Sphagnum* (Figure 40-Figure 42), *Calymperes* (Figure 43-Figure 49), or *Polytrichaceae* (Figure 28-Figure 34), the leaf architecture in *Pottiaceae* (Figure 45-Figure 48), the large size of *Dawsonia superba* (Figure 50) versus the minute size of *Stonea*, *Goniomitrium* (Figure 51), or *Weisiopsis*, the structure of *Ephemeropsis* (Figure 52), the size of some plants of *Fontinalis* (Figure 53), the variation in peristome morphology, variety of vegetative propagules, costal anatomy, cell architecture, a life history that may go from spore to spore in less than 2 weeks. Think of the adaptations of *Splachnaceae* (Figure 54) for attracting insects and spore dispersal, bryological physiological capabilities (desiccation, living in water, salt tolerance, tolerance in some of heavy metals etc.) - and that is without delving into the liverworts (some of which live in highly acidic fumarole streams) and hornworts.



Figure 39. *Sphagnum contortum*, a moss of fens and mires. Photo by Jan-Peter Frahm, with permission.



Figure 40. *Sphagnum cuspidatum*, a moss of bog and fen pools and lakes. Photo by Aimon Niklasson, with permission.



Figure 41. *Sphagnum angustifolium* Europe 3 Photo by Michael Lüth, with permission.



Figure 42. *Sphagnum girgensohnii*, a moss that is common in coniferous forests. Photo by Janice Glime.



Figure 43. *Calymperes tenerum* with gemmae. Photo by Jan-Peter Frahm, with permission.

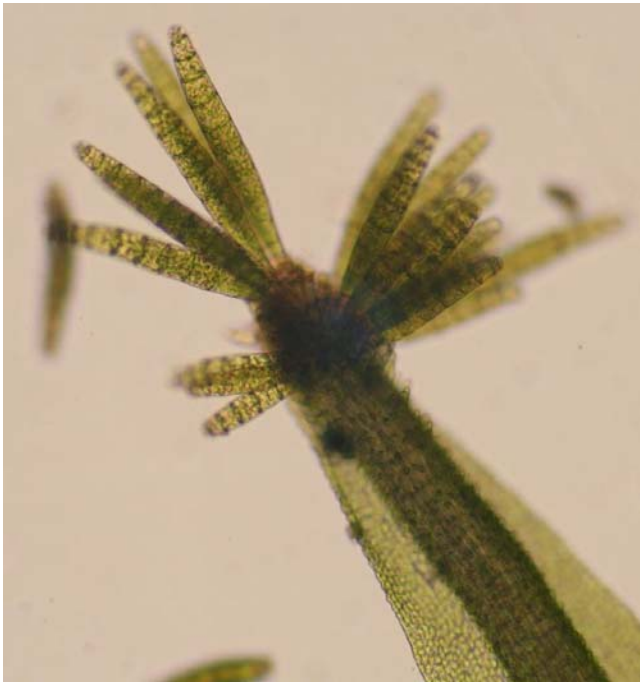


Figure 44. *Calymperes erosum* leaf with gemmae. Photo by Li Zhang, with permission.



Figure 45. *Aloina ambigua* showing succulent leaves. Photo by John Game, through Flickr Creative Commons.



Figure 46. *Anoetangium aestivum* showing diversity in the Pottiaceae. Photo by Michael Lüth, with permission.



Figure 47. *Tortella fragilis*, a member of the Pottiaceae showing fragile leaf tips. Photo by Michael Lüth, with permission.



Figure 48. *Syntrichia intermedia*, a member of the Pottiaceae with long leaf awns. Photo by Jan-Peter Frahm, with permission.

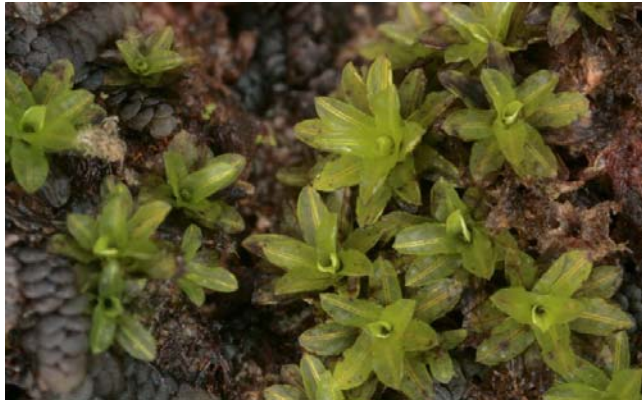


Figure 49. *Calymperes motleyi*. Photo by Jan-Peter Frahm, with permission.



Figure 50. *Dawsonia superba* from New Zealand. Note the ferns between the plants in the foreground, giving reference to the large size of *Dawsonia*. Photo by Jan-Peter Frahm, with permission.



Figure 51. *Goniomitrium enerve*, a very tiny moss. Photo by David Tng, with permission.



Figure 52. *Ephemeropsis trentepohlioides*. Photo by Niels Klazenga, with permission.



Figure 53. *Fontinalis duriaei* showing long, dangling plants; held by Janice Glime. Photo by Zen Iwatsuki, with permission.



Figure 54. *Splachnum rubrum* showing expanded and colorful hypophysis on capsule, used for attracting flies. Photo by Michael Lüth, with permission.

In the case of the bryophytes, as Diego has pointed out, physiological adaptations/modifications may be as important or more important. Bryophytes have such wonderful abilities to dry out and then revive that researchers in agriculture have been attempting to put the bryophyte genes into tobacco, among other things.

To quote Seppelt, "What could be more physiologically challenging than living in acid water (*Solenostoma vulcanicola*), occasional immersion in sea water [*Muelleriella crassifolia* (Figure 55)], or sitting on a rock or desert soil pavement where the diurnal temperature and moisture regime can go from being frozen overnight, being wet from dew in the morning, dehydrate in the sun during the day when soil or rock surface temperatures can reach well in excess of 40°C, becoming moist again in the evening with dew, and refreezing overnight.



Figure 55. *Muelleriella crassifolia*, a moss with a rare tolerance to submersion in sea water. Photo by Juan Larrain, Cape Horn Bryophytes NYBG, with permission.

Perhaps one constraint on morphological diversity is that genes for the gametophyte and for the sporophyte are subjected to different selection pressures (Pokorny *et al.* 2012). If these genes occur on the same chromosomes, selection will work against the greater of two evils, permitting somewhat unfit characters to persist because their chromosomes are needed in the other generation. For example, Pokorny *et al.* (2012) found that in the **Hookeriales** both sporophyte and gametophyte characters are labile, with documented parallel changes and reversals in traits from both generations.

By the time bryophytes evolved, algae already had the five hormones known from plants (Tarakhovskaya *et al.* 2007). But these are hormone groups, and variations within them were on the way. Furthermore, coordination that worked in water might often fail on land due to absence of sufficient water at a critical time. Perfection of timing would necessarily take a long history of trial and error among the species in the many new habitats. And such timing coordination would require enzymes and other forms of controls, responsive to the new cues of the terrestrial environment. Many changes were needed for a diverse and increasing array of niches.

Summary

Sporophytes are perched atop the gametophyte and are dependent on them. This means that they must live with the selection pressures that determine selection on the gametophyte.

Sporophytes begin in the archegonium, which breaks apart to become the calyptra on the upper part of the sporophyte. This gametophyte calyptra structure, surrounding the developing sporophyte, influences its development. The calyptra can completely cover the capsule, be split on one side, or sit only as a short covering at the top. The calyptra may have hairs that may cease importance after the embryo emerges from the base of the archegonium or that may develop further to reduce water loss or defer herbivores.

Capsule stomata occur at the base of the capsule in many genera of mosses and hornworts, but not in liverworts. They may provide openings for CO₂ exchange during early development or permit faster drying to aid spore dispersal. They may open and close in the young capsule; they may remain open in the older capsule; they may become non-functional with the stoma closed with wax at later stages.

Bryophytes have been considered slow evolvers, simple plants. But evidence suggests that they evolve at rates similar to those of other plants. Lack of lignin limits size and small size limits morphological development. But bryophytes invented numerous controls that are timed with environmental changes such as seasons, they developed a range of new hormones, and they developed numerous secondary compounds that protect them from herbivory, bacteria, and fungi. Furthermore, they have interesting mechanisms by which they survive desiccation and winter freezing conditions while their photosynthetic tissue remains above ground. They are not without morphological variability, as demonstrated in Chapter 4-12.

These adaptive values of bryophyte structures are largely speculation, hypotheses waiting to be tested.

Acknowledgments

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